Final Report

Ecological Study of peat landforms in Canada and Alaska

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Ecological Study of Peat Landforms in Canada and Alaska

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1. Introduction

Over 20% of the land surface of Canada and Alaska is covered by peatlands, which may be defined as any waterlogged ecosystem with a minimum thickness of 20 cm of organic matter in the soil (Kivinen and Pakarenin 1981). Although peatlands are common throughout the boreal region, the majority of peat is concentrated in a few major peat basins located within the continental interior of Canada and Alaska (Zoltai and Pollet 1983; Glaser 1987a; Fig. 1). Here peat has spread over the regional landscape, restricting exposures of mineral soil to isolated locations. These large peat basins represent one of the most important reservoirs in the global cycle for carbon and may also be the most significant source for atmospheric methane (Matthews and Fung 1987; Sebacher *et al.* 1986). However, field work has been limited in these large peatlands because of their great expanse of roadless, waterlogged terrain. The important ecologic and hydrogeochemical processes that control the development of these peat basins therefore have been largely inferred from studies of much smaller peatlands, which have a much different ecologic and hydrologic setting.

Past investigations have demonstrated the value of aerial photographs in identifying the major vegetation types and analyzing the biotic and hydrogeologic processes that control the development of these peatlands (Glaser *et al.* 1981; Glaser 1987a,b). In the present study, Landsat TM imagery was used in conjunction with field studies to determine the utility of this satellite sensor for detecting these important processes.

2. Target Areas

Target areas were selected in three of the largest peat basins in North America 1) the Glacial Lake Agassiz region, 2) the Hudson Bay lowlands, and 3) the Great Slave/Great Bear Lake lowlands (Zoltai and Pollet 1983; Glaser 1987a; Fig. 1). Very large peat deposits are also present in the interior of Alaska, which were not included in this study. The 3 target areas are situated in regions of relatively low relief and are underlain by largely

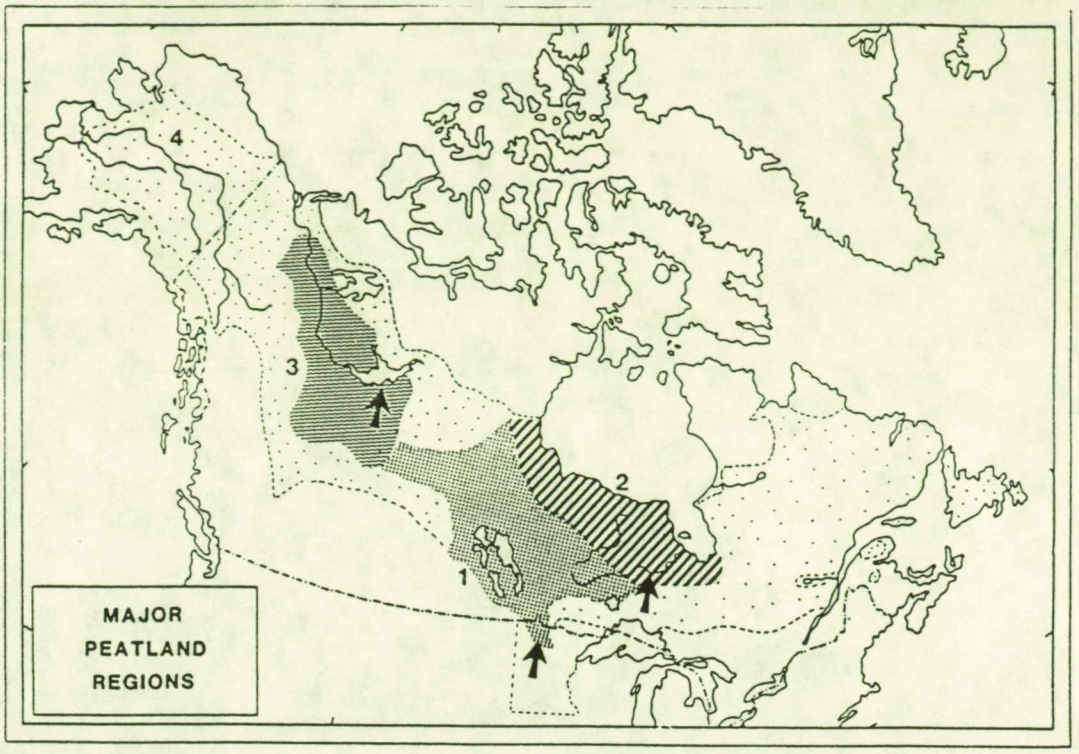


Figure 1. Major peat basins in North America. The largest peat basins are 1) the Glacial Lake Agassiz region, 2) the Hudson Bay lowlands, 3) the Great Slave Lake lowlands, and 4) the interior of Alaska. The stippled area represents the boreal region. The target areas are marked by arrows.

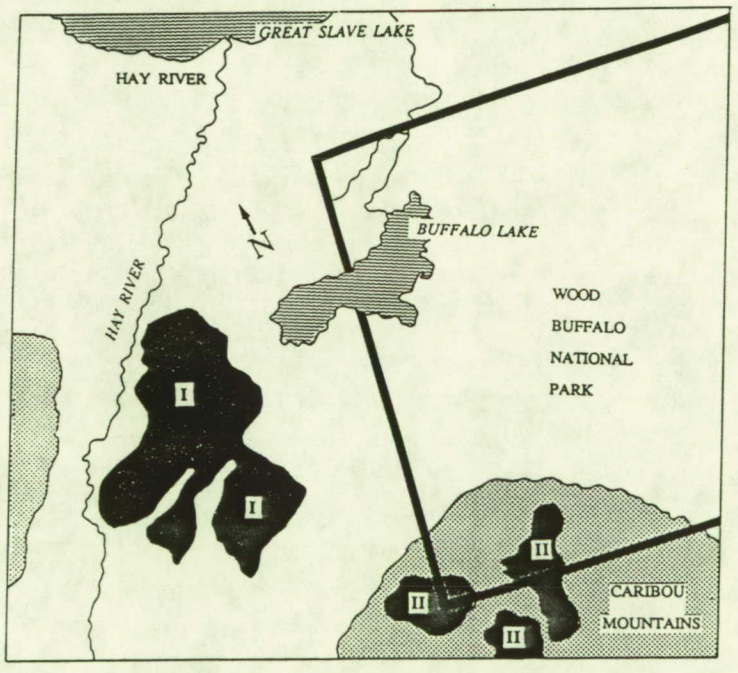


Figure 4. The Hay River target area. The peatland watersheds selected for study are I) lowland peat plateaus complexes and II) highland peat plateaus. The Caribou Mountains and other highlands are indicated by light stippling. This figure corresponds to a Landsat TM scene (E-50460-18221; Path 46, Row 18) and has a scale of approximately 1: 1,000,000.

calcareous sediments (Bostock 1967; Wright and Glaser 1983). Each target area corresponds to a Landsat TM scene and represents an important reference point along important ecologic and climatic gradients.

2.1. Glacial Lake Agassiz Area

The first target area is located in the Glacial Lake Agassiz region of northern Minnesota and southwestern Manitoba (48° - 55° N. Lat. and 93° - 96° W. Long.). The large peatlands in this area are dissected by linear exposures of loamy ground moraine or sandy beach ridges deposited by Glacial Lake Agassiz (Fig. 2). The climate is continental, with a summer maximum in precipitation. Permafrost is absent from the region and apparently was never associated with the development of these peatlands, which started to form after the mid-Holocene, approximately 4500 yr B.P. (Heinselman 1963; Janssen 1968; Griffin 1977; Glaser *et al.* 1981).

2.2. Albany River Area

The second target area is located within the Albany River drainage in the Hudson Bay lowlands and approximately corresponds to the Ghost River Map area (51° - 52° N. Lat. and 82° - 83° W. Long.). This area is covered by a nearly continuous blanket of peat except for small local exposures of mineral soil and many small lakes (Fig. 3). The most prominent physiographic features are 1) a moraine system in the southwestern portion of the study area, 2) nearly featureless plains along the edge of the moraine system, and 3) plains dissected by numerous streams with branching tributaries. The climate is colder and drier (15 - 81 cm) than that to the south, but permafrost is absent from the study area. The peatlands started to form approximately 6000 yr B.P. following the draining of Glacial Lake Agassiz and the Tyrrell Sea (Sjörs 1963). Paludification, however, is still occurring along the coast, which continues to emerge in response to isostatic rebound (Dionne 1979).

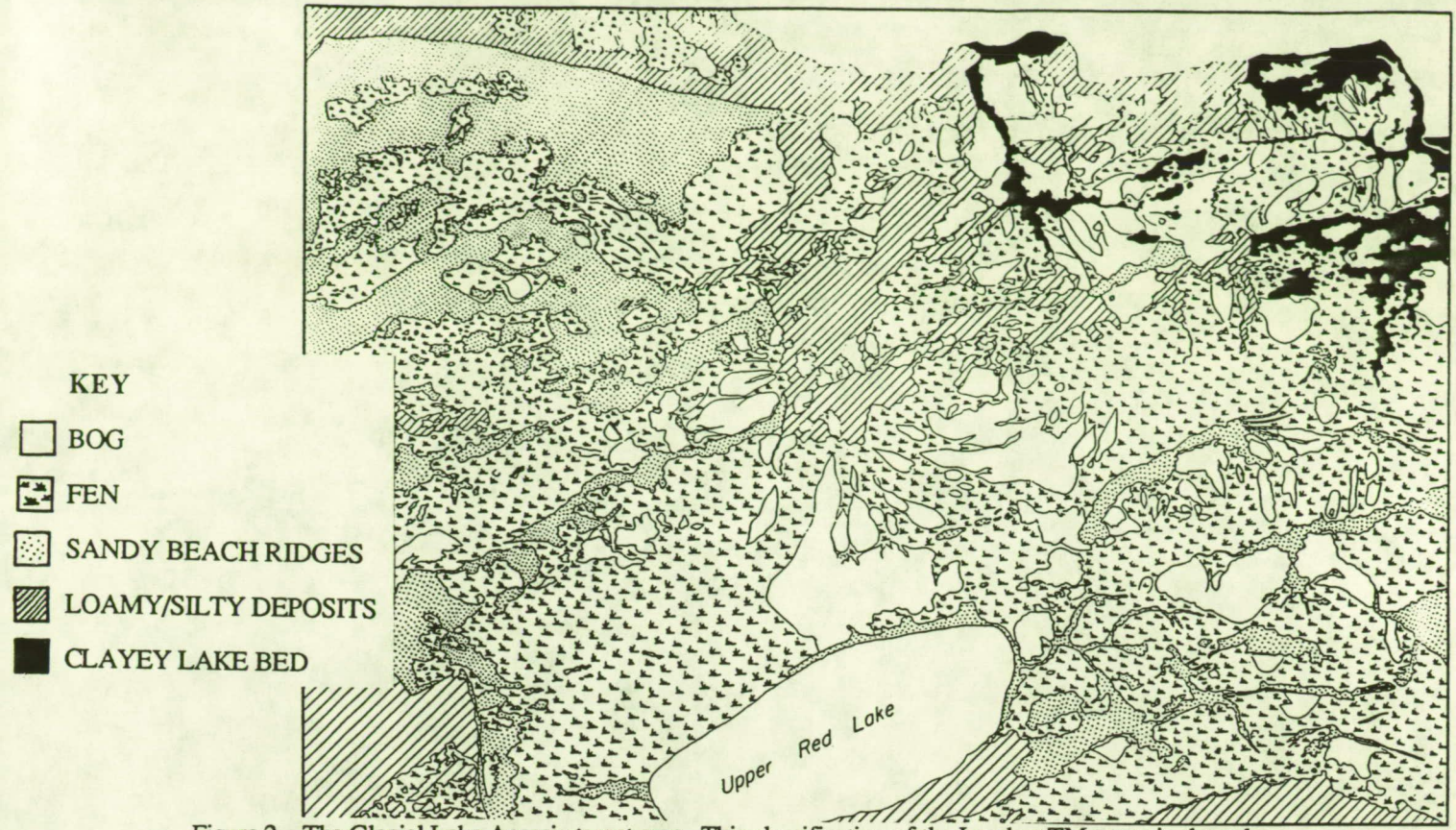


Figure 2. The Glacial Lake Agassiz target area. This classification of the Landsat TM scene in the color centerfold distinguishes 1) fen vegetation, 2) bog vegetation, 3) exposures of sandy soil, 4) exposures of loamy soil, 5) exposures of clayey soil, and 6) areas with standing water. Most of the peatlands in this scene are fens, although the bog-dominated areas are primarily located in the NE quadrant where the smaller peatlands are surrounded by relatively impermeable clayey or loamy soils. The large tracts of fen vegetation, in contrast, are located in areas with exposures of permeable sandy soils.



Figure 3. The Albany River study area. This classification of a Landsat TM scene separates bog vegetation (white), fen vegetation (grey), and standing water (black). The largest bogs are located on the dissected plain to the left, whereas large stands of fen occur downslope from the moraine complex to the right. Calcareous groundwater apparently discharges along the edge of the moraine complex and maintains these large areas of fen. The target area for this classification scene covers 8,400 km^2.

2.3. Hay River Area

The third target area is located in the Hay River drainage south of Great Slave Lake (114° - 115° N. Lat. and 59° - 61° W. Long.). This area is largely composed of a paludified plain and several flat-topped hills that rise approximately to 950 m in elevation (Fig. 4). It is underlain largely by limestone and dolomite and was inundated by Glacial Lake McConnell until 10,000 yr B.P. (Bostock 1967; Dyke and Prest 1987). The climate is colder and drier than that of the other target areas, and permafrost is common in the bogs. Peatlands began to form in this region during the early Holocene, but the major period of peat accumulation occurred between 8000 and 5000 yr B.P. (Zoltai and Tarnocai 1975).

3. Methods

Each target area was first analyzed with black and white aerial photographs prior to field work. These images ranged in scale from 1:15,000 to 1:40,000 and were used to identify potential sites for field sampling. During the summers of 1985 and 1986, field work was conducted in each target area to identify the major patterns in the vegetation, water chemistry, and peat stratigraphy. The methods used for these investigations follow Glaser *et al.* (1981) and Glaser (1983a). A helicopter or float plane provided comprehensive access to the study area. In the Albany River region it was necessary to set up a base camp within the peatlands because of the remote setting of the site.

An intensive hydrogeochemical study was conducted in the Lost River peatland in northern Minnesota to determine the role of groundwater hydrology on the development of the landform patterns. Nests of piezometers were installed at the crest of a raised bog and adjacent spring fen mound to determine gradients in hydraulic head and to sample pore-water. Peat cores from this site were also analyzed to reconstruct the development of this peatland.

Images of the target areas were then processed from Landsat TM imagery at the Goddard Space Flight Center. The scenes used were 1) L5TM8553000 (8-3-86) and

L5TM5130116371 (9-23-87) for the Glacial Lake Agassiz region, 2) E-40062-15532 (9-16-82) for the Albany River region, and 3) L5TM8744 (6-4-85) for the Hay River region. The most useful information was obtained from false color composites using TM bands 2, 3, and 4 (=blue, green, and red) with a linear contrast stretch. False color composites using bands 3, 5, and 4 (=blue, green, and red) were also processed. An unsupervised classification using the isoclass routine from LAS (Land Analysis System) was also conducted on a subscene from the Albany River target area. The 15 classes identified from this analysis were then merged by a supervised classification into 3 classes that correspond to areas of bog, fen, and standing water.

A supervised classification was conducted of the major peatland types within the Glacial Lake Agassiz regions using large 20 x 30" prints of Landsat images of the target area. Outlines of the major vegetation types were traced onto mylar overlays, whereas the major soils were determined from existing soil and surficial geology maps.

The morphometry of the peat landforms were analyzed to infer the processes that control their development. The principal dimensions of 40 bog islands were determined with an X-plan 360 computer curvimeter. The length of these islands parallels the main direction of flow, the width as the maximum line drawn perpendicular to the length, and the area as the space enclosed within the margins of the island. The island dimensions were quantitatively studied by transforming these data to logarithms and calculating linear regressions of the length vs. area, width vs. area, and length vs. width.

The relative area of bog and fen were determined for 59 peatlands in northern Minnesota with an X-plan 360 computer curvimeter. These data were quantitatively studied by calculating linear regressions of the area of bog vs. total peatland area, area of fen vs. total peatland area, and bog-to-fen ratio vs. total peatland area, and by comparing these data to regional changes in soils, physiography, and climatic isopleths.

4. Results

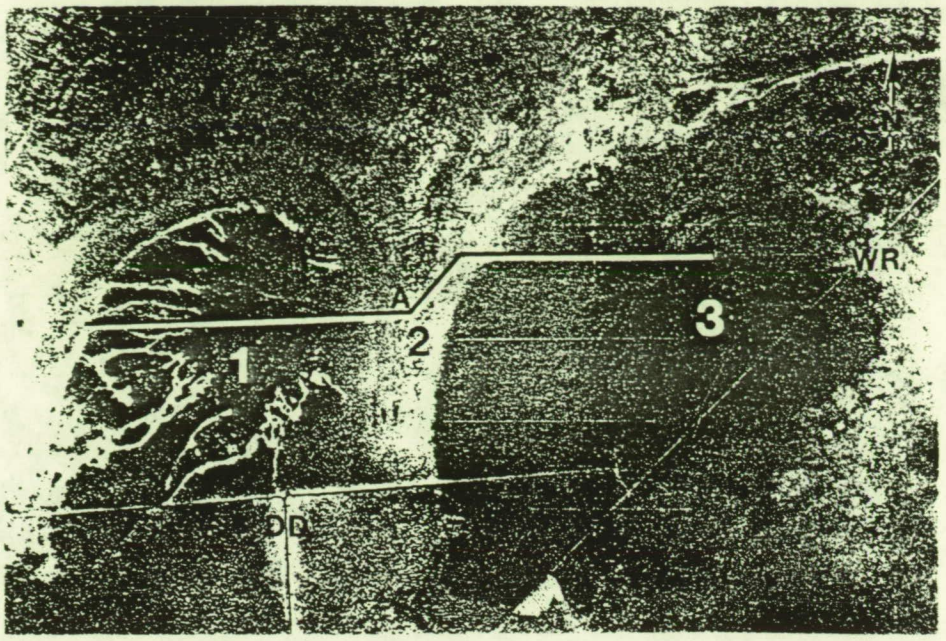
4.1. Peat Landforms

The vegetation within these large peat basins has developed into orderly geometric shapes that simulate the form of geomorphic landforms, such as river channels, streamlined islands, and networks of ripples (Glaser 1987a, b; Fig. 1). These patterns seem to be products of sensitive feedback systems that involve 1) vegetation processes, 2) differential peat accumulation, and 3) hydrology. Because of their consistent shape over broad geographic areas, and their relatively uniform species assemblages these patterns can best be described as peat landforms.

4.1.1. Peat Landforms as Ecological Units.

The vegetation patterns in boreal peatlands are commonly called peat landforms because of their visual similarity to geomorphic landforms. A peat landform is characterized by 1) its characteristic shape in cross-section and plan view, 2) a distinct vegetation assemblage, and 3) narrow ranges in water chemistry (Glaser *et al.* 1981; Glaser & Janssens 1986; Glaser 1987a). Certain types of landforms are also highly characteristic of discharge areas for groundwater (Tarnocai 1974; Glaser 1983b; Glaser *et al.* in press).

Each type of landform has a characteristic Grossform (cross-sectional profile) and Kleinform (surface pattern) (Aario 1932; Paasio 1933; Glaser & Janssen 1986). A peat landform is therefore a 3-dimensional feature, which is composed of living vegetation on the surface of a massive deposit of organic matter (Fig. 5). These 2 components of a landform are highly correlated. The surface features visible on aerial photographs (plan view) are consistently oriented according to the prevailing slope. This relationship has been demonstrated by careful topographic leveling in Fennoscandia, eastern Canada, and Minnesota. The scales of these 2 components, however, are not comparable. Surface relief rarely exceeds 1 meter/kilometer in Minnesota and is often less than 50 cm/kilometer. In plan view, however, a peat landform can cover an area up to 140 km^2 in Minnesota.



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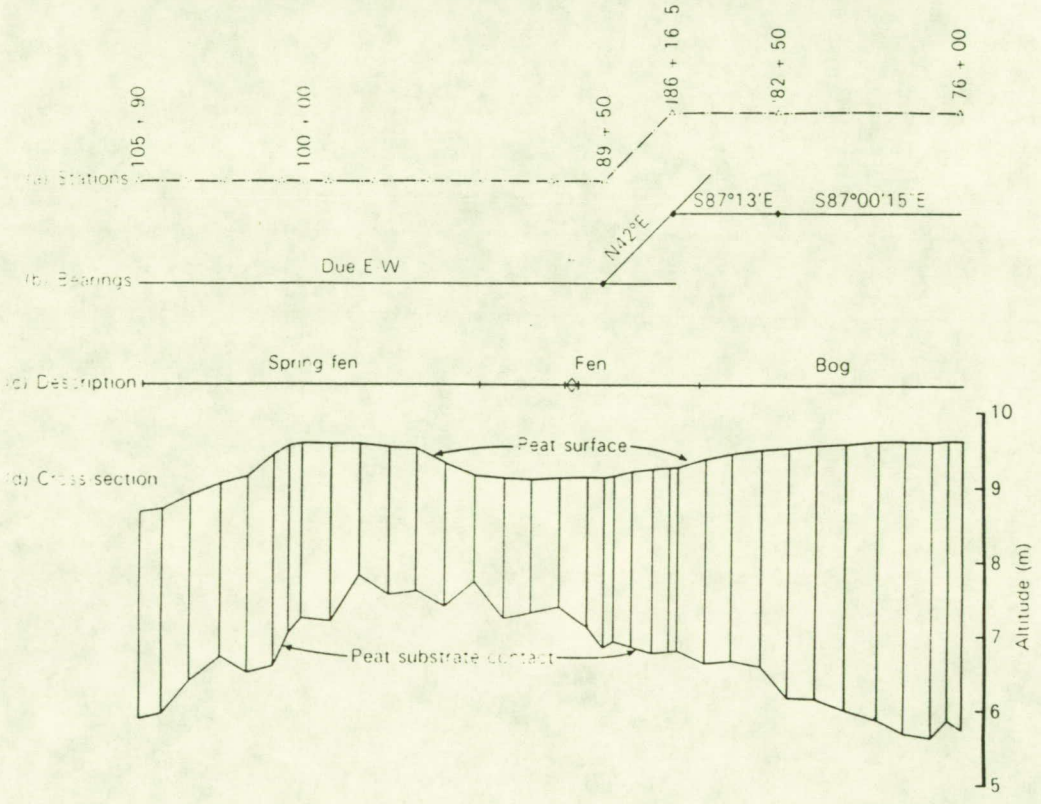


Figure 5. Peat landforms in the Lost River peatland. Peat accumulation produced 3 types peat landforms 1) a spring-fen mound, 2) a water track, and 3) a raised bog. The surface elevations of the 2 peat mounds is nearly identical, although the spring-fen mound has developed over a rise in the mineral substratum, and the raised bog has developed over a depression (Almendinger *et al.* 1986; Glaser *et al.* in press).

Although the surface area of raised bogs and water tracks is usually greater in the the Hudson Bay lowlands and Hay River region the surface relief of these landforms is comparable to that in Minnesota. A bog complex along the Albany River, for example covered over 20 km^2, whereas its surface elevation rose less than 2.5 m from the bog margin to the nearly level bog plain (Fig. 6).

Each of the different landform types in the target areas is associated with different ranges in water chemistry and different assemblages of species. The peat landforms therefore provide an important indicator of the peatland environment. The patterns also provide important new data on peatland development. Spatial transitions from one type of landform to another may represent important developmental trends, which can be tested by the stratigraphic analysis of peat cores (Glaser *et al.* 1981; Glaser 1987a,b). The physical dimensions of the landforms (length, width, and area) can also be measured and analyzed to infer the processes that formed them (Glaser 1987a).

4.1.2. Peat Landform Types

Four basic types of peat landform occur in the target areas: raised bogs, peat plateaus, water tracks, and spring-fen channels. These landform types are closely related to the principal types of peatland vegetation, which are discussed in more detail in the next section. Raised bogs have a raised profile in cross section, which isolates the bog surface from solute-rich runoff draining from the surrounding mineral uplands. In northern Minnesota raised bogs have a forested crest from which lines of spruce trees radiate downslope (Heinselman 1963, 1970). This pattern produces the characteristic radiating forest patterns that appear on aerial photographs (Fig. 7). On the lower bog flanks the spruce forest gives way to nonforested lawns, which form an apron around the forested crest. In large peatlands raised bogs have a streamlined margin, where they are trimmed by fen vegetation. These streamlined forms simulate the shape of islands where the bog is completely surrounded by fen vegetation.

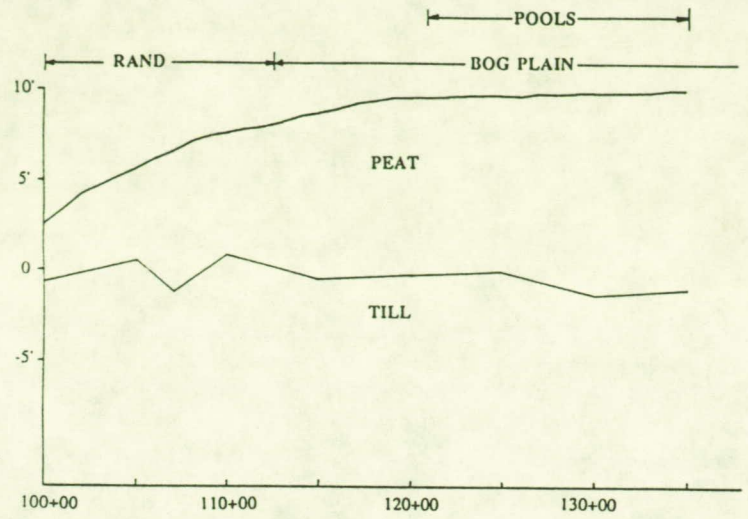


Figure 6. Cross-sectional Profile from a raised bog along the Albany River

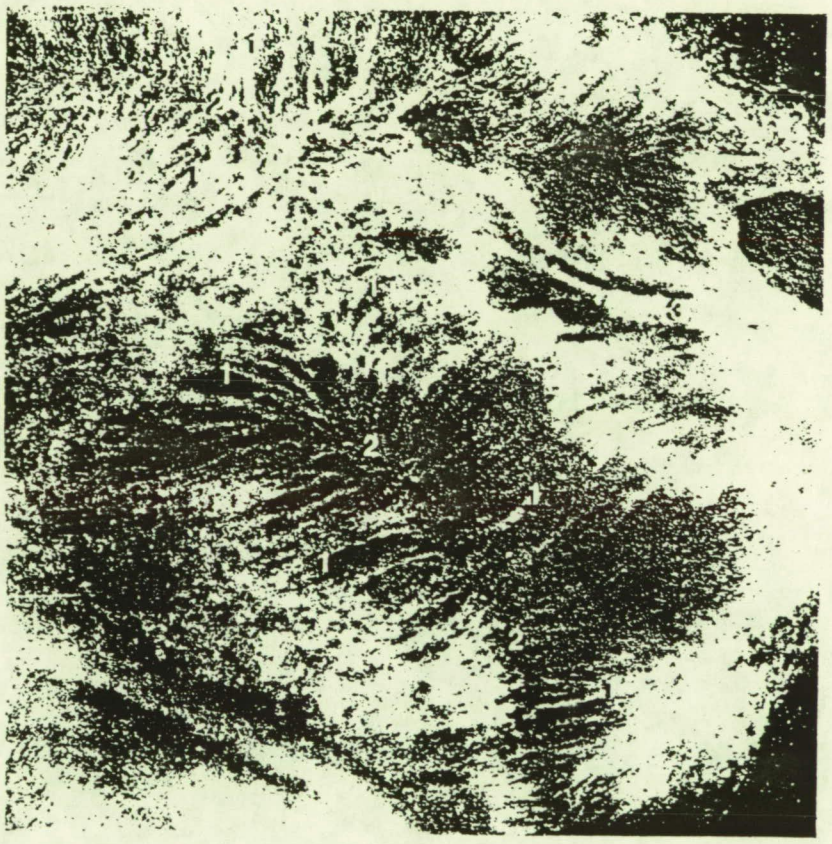


Figure 7. A raised bog with radiating forest patterns. The bog is distinguished by lines of spruce trees (1), which radiate from the central bog crest (2). The lower flanks of the bog are fringed by a nonforested *Sphagnum* lawn (3). This aerial photograph of the Myrtle Lake peatland covers an area 2.5 km across.

In the Albany River region a transition occurs as the forest cover on raised bogs gradually disappears and the nonforested bog plain is marked by intricate networks of pools(Glaser and Janssens 1986; Glaser 1987a) (Fig. 8). No permafrost was found in these bogs. The bogs are replaced farther north by peat plateaus that are underlain by permafrost (Fig. 9). Peat plateaus contain stunted spruce trees and are pock-marked by thermokarst collapse scars in the Hay River region (Glaser 1987a). The collapse scars occasionally contain water but are usually carpeted by flat *Sphagnum* lawns.

Water tracks (Sjörs 1948), in contrast, have a concave to flat profile in cross section and represent zones where runoff is channeled across the peat surface. Water tracks have the appearance of river channels on aerial photographs and are sharply delineated from the surrounding vegetation, which generally consists of swamp forests or raised bogs (Fig. 10). Three types of water tracks are found in the target areas (Glaser 1987b). Featureless water tracks contain linear bands of trees and shrubs that are oriented parallel to the prevailing direction of flow. They usually consist of nonforested sedge meadows that are surrounded by wet swamp forests. Patterned fens (Aapamoor or Strangmoor of Fennoscandian authors) are water tracks that contain distinctive networks of peat ridges (strings) and pools (flarks) arranged perpendicular to the slope. Patterned fens may also contain fields of tree islands, which are oriented parallel to the prevailing slope (Fig. 11). These islands always have rounded heads and tapering tails that stream downslope.

The water tracks in the Albany River region are distinguished by their deep pools that in places approach the size of small lakes. These features represent a regional trend in which the pools in water tracks enlarge in peatlands of greater age. Water tracks with reticulate networks of pools and peat ridges also occur in this region but are more typical of the Hay River target area near Great Slave Lake.

The fourth type of peat landform is the spring-fen, which is similar to water tracks with tree islands (Fig. 12). Spring-fens consist of an anastomosing network of nonforested channels that drain through a swamp forest and carry alkaline water. The forest is

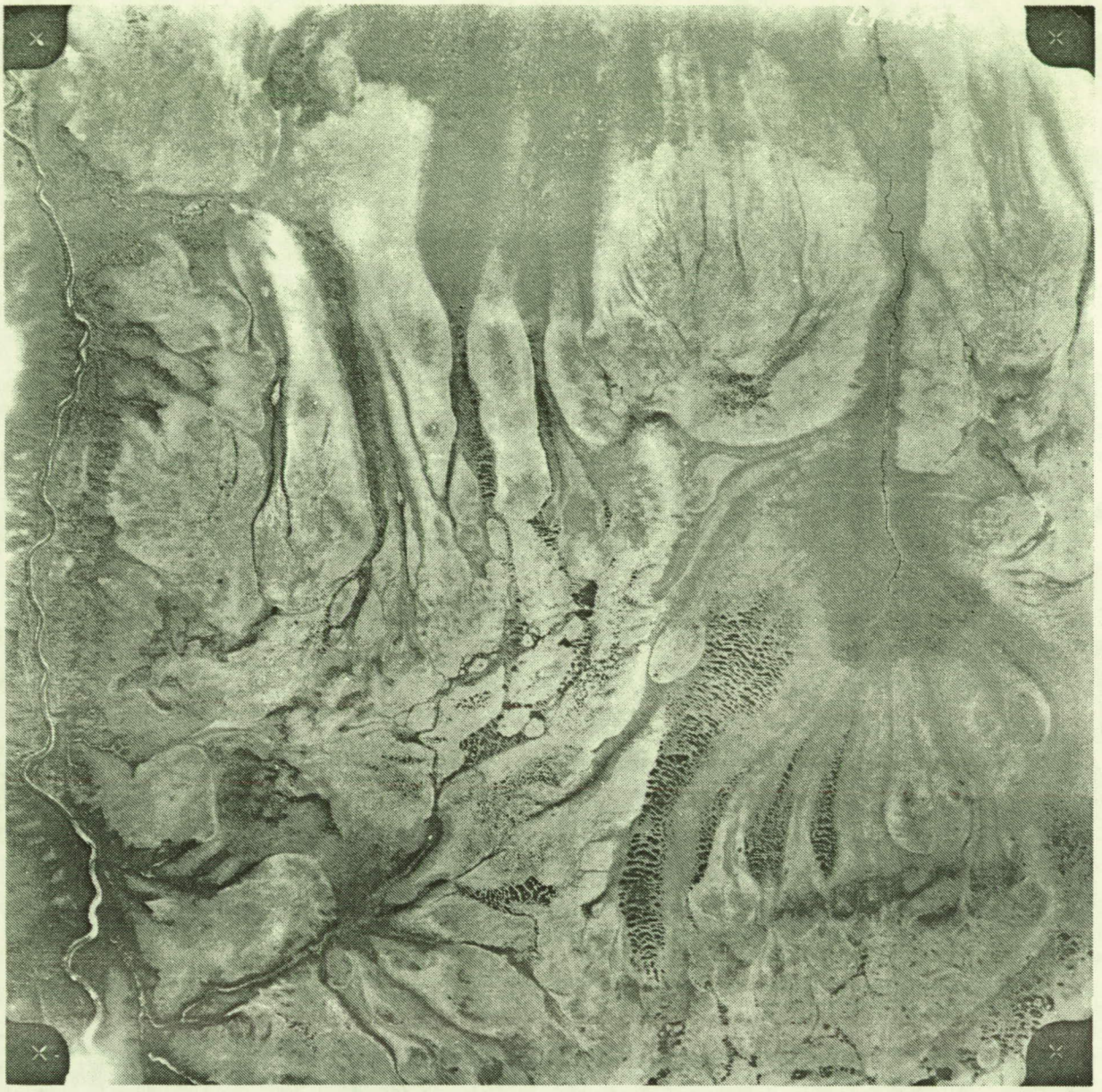


Figure 8. Peat landforms in the Albany River study area. The large raised bogs (1) are distinguished by their light tones and streamlined margins where they are trimmed by water tracks (2). The bogs are fragmented by smaller water tracks (3; dark tones) and large pool systems (5). The peatland is drained by small streams (6). The photo covers an area approximately 16 km across.

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Figure 9. Lowland peat plateaus near the Hay River. The peat plateaus are dissected by water tracks (↓) that divide the lower bog flanks into streamlined lobes (2) and bog islands (3). The mottled appearance of the peat plateaus is produced by the numerous thermokarst collapse features. Water drains toward the upper part of the photo, which covers an area about 6 km across.

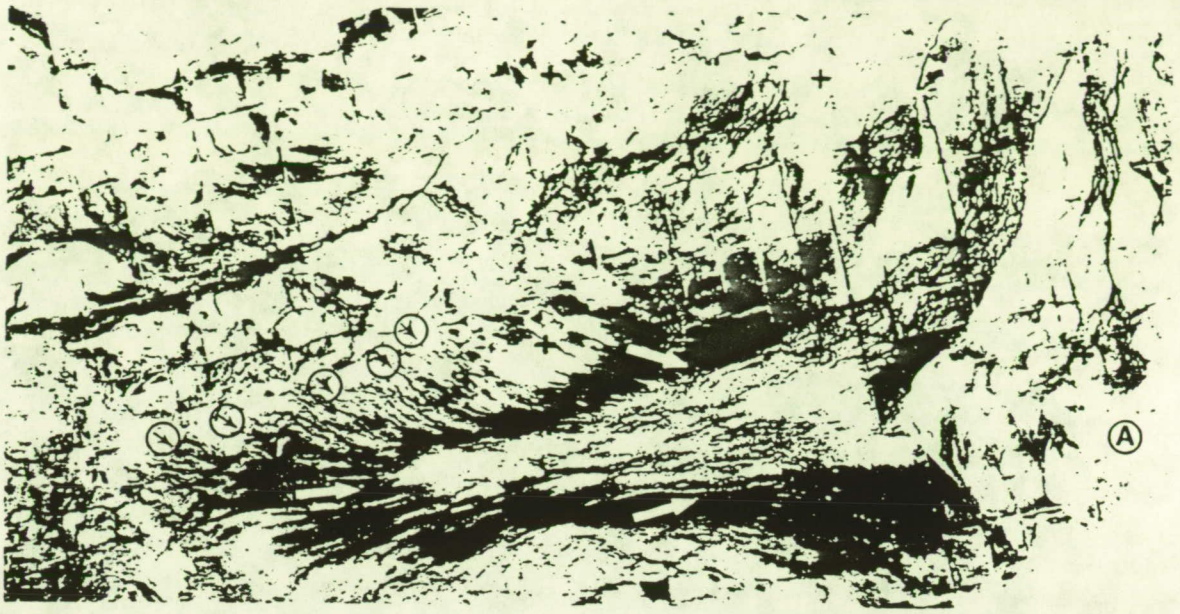


Figure 10. Landsat MSS image of the western water track of the Red Lake peatland. This image (E-30042-16303-D) was recorded during spring break-up in 1978. The water track (large white arrows) drains eastward to a large raised bog complex (A), where it splits into two diverging branches. Surface drainage (darker tones) arises in narrow channels (small dark arrows) downslope from a beach ridge and flows around the central portion of the track, which is still ice-covered (white tone). Surface drainage on the adjacent bog (A) is also focused in internal water tracks (dark grey tones), in contrast to the surrounding snow-covered bog areas (white). The rectangular lines are drainage ditches spaced 1.6 or 3.2 km apart. Most of the image is covered by peatland except for the snow-covered beach ridge north of the western water track. The image covers an area approximately 64 km across. See color plates 5-7 for comparison.

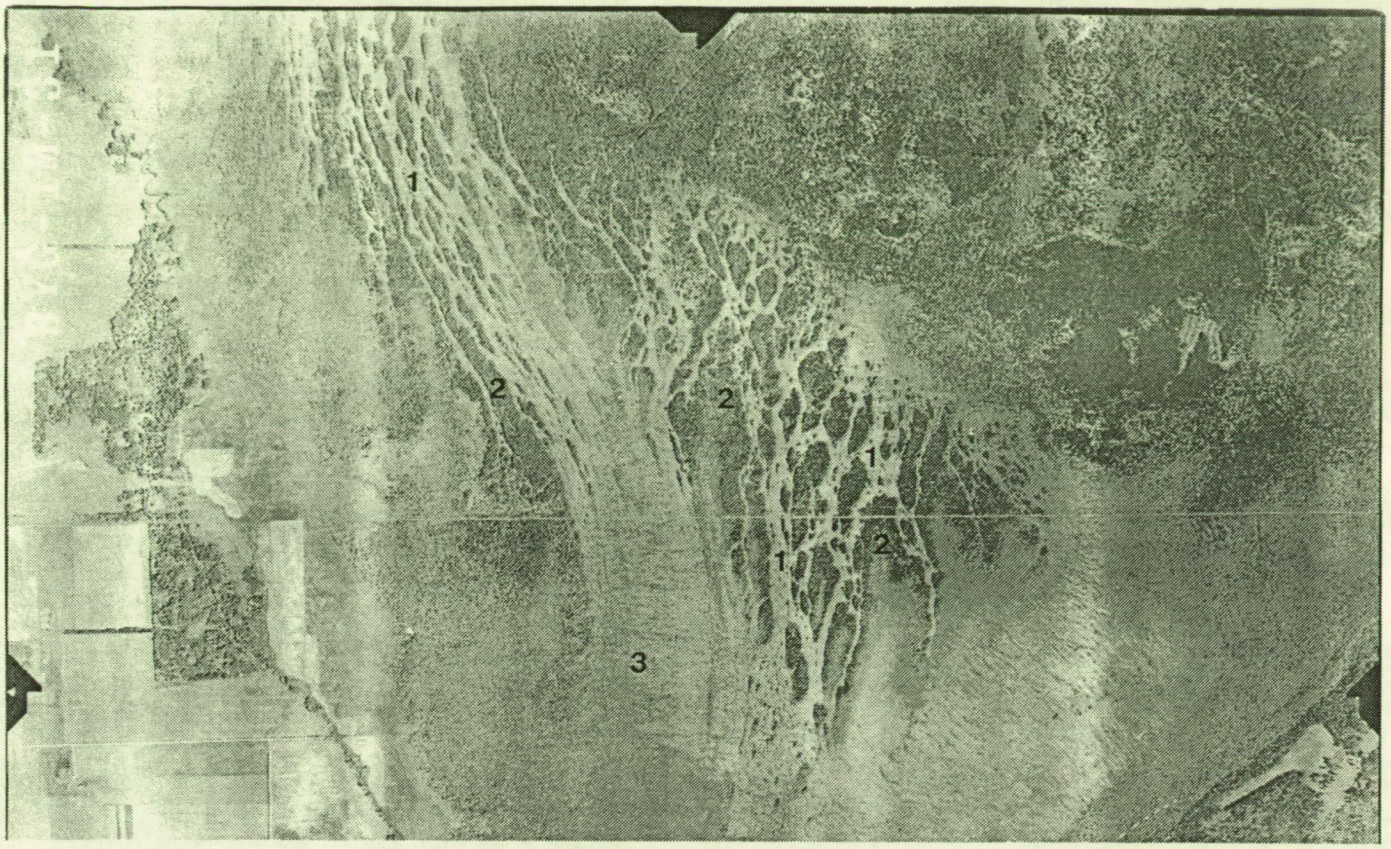


Figure 12. Spring-fen channels near Pine Creek. The peatland is characterized by an anastomosing network of channels that drain southward through a swamp forest. The forest is fragmented downslope into long tapering fingers and discrete tree islands.



Figure 11. Peat islands in the Hay River area. The streamlined peat islands are underlain by permafrost and completely surrounded by water tracks.

generally fragmented downslope into long streamlined fingers that split off into distinct tree islands. Spring fen landforms are found in all 3 target areas.

4.1.3. Mire-Complex Types

Most of the larger peatlands in the target areas contain more than one landform type and may best be described as mire complexes (*sensu* Cajander 1913). Mire complexes can be classified according to 1) their size and 2) the configuration of bog, fen, and mineral soil in a watershed. Most mire complexes in northern Minnesota are clearly separated from adjacent peatlands by mineral soil. The borders of these discontinuous complexes (types 1-7) are easier to delineate than the continuous complexes (types 8-11) of the other target areas in which the watershed divides are often covered by peat (Figs. 13-14). However, the drainage divides in these continuous peatlands may be determined by the vegetation patterns that are sensitively adjusted to the prevailing direction of water movement.

The simplest mire complex type (1) consists of a single bog that almost completely fills the peatland except for a narrow marginal lagg. These mire complexes are generally small (<20 km^2) and either straddle drainage divides or contain only a narrow strip of mineral soil at the crest of the watershed (Fig. 13). The bogs in these complexes may completely surround small lakes or outcrops of mineral soil.

In larger mire complexes (>20 km^2) the raised bogs are separated by water tracks of varying sizes. The water tracks originate in drainage channels at the mineral crest of the watershed and terminate in tributary streams at the downslope margin of the peatland. The bogs, in contrast, are located downslope from flow obstructions or develop over minor drainage divides. The majority of these mire complexes contain less than 50% bog and are smaller than 50 km^2 (Fig. 15). A few complexes, however, are huge, ranging up to 180 km^2. Despite these physiographic constraints most bog and fen patterns can be assigned to a limited number of types.

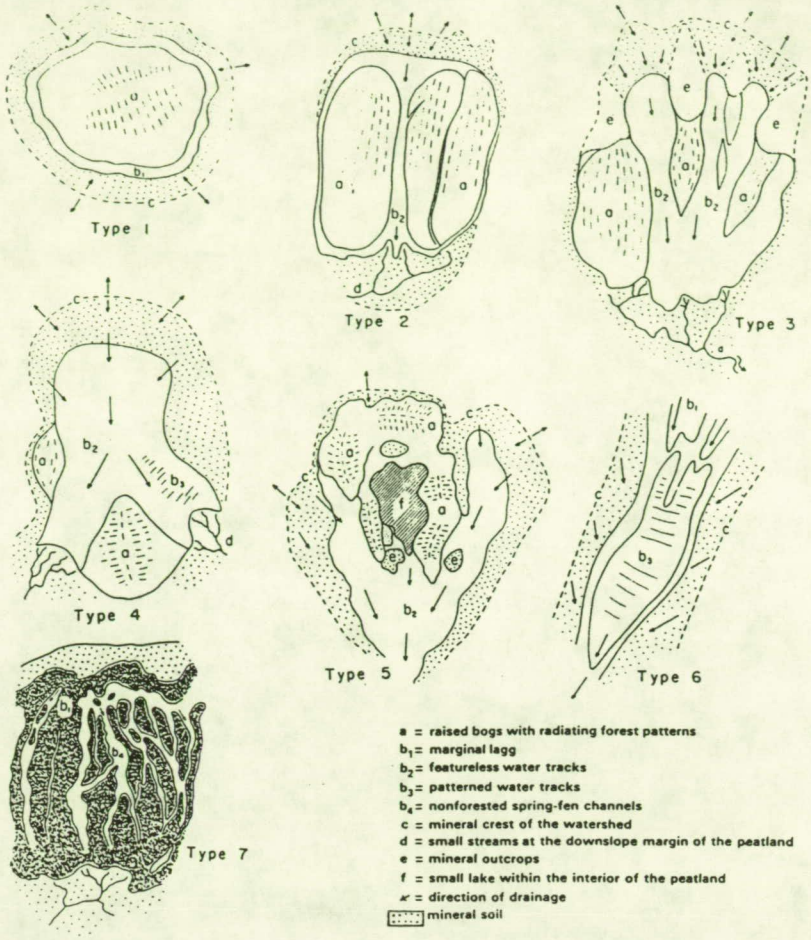
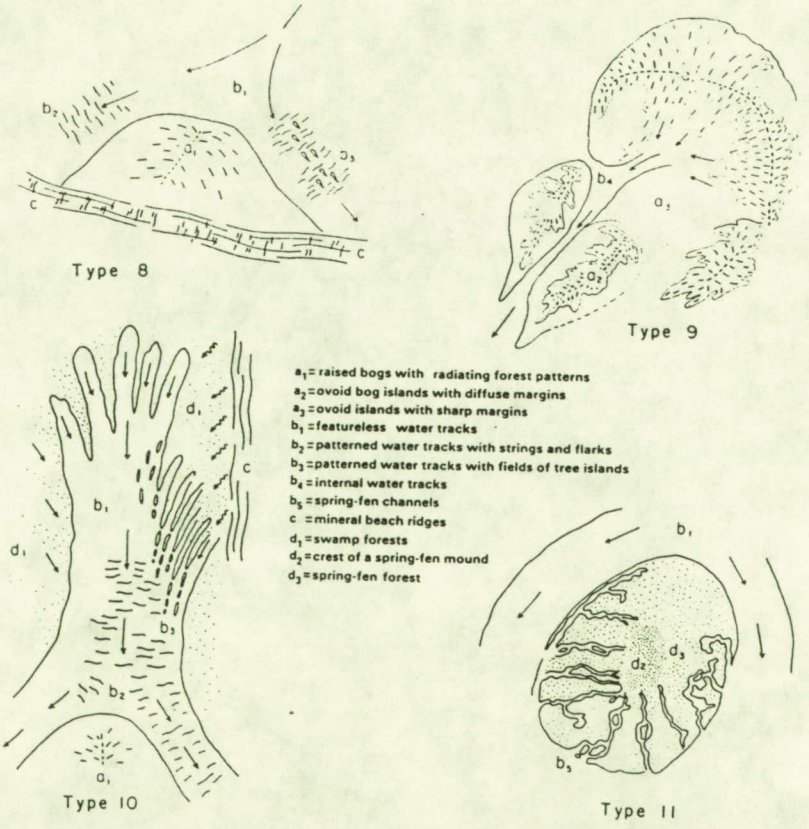


Figure 13. Discontinuous mire-complex types. The types represent reference points along a continuous range of variation (Glaser 1987b, in press). In types 1-5 the area of fen relative to bog increases, culminating in the very large water tracks of type 4 (Glaser 1987a). The arrows show the direction of water movement.



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Figure 14. Continuous mire-complex types in Minnesota (Glaser 1987a, in press).

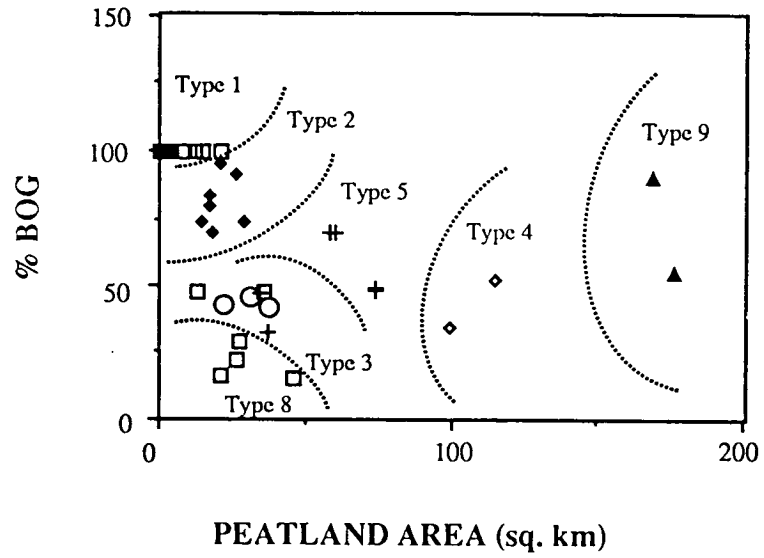


Figure 15a. Dimensions of selected mire complex types in Minnesota. Mire-complex types may be categorized according to their proportion of bog or fen in relation to the total area of peatland (Glaser in press).

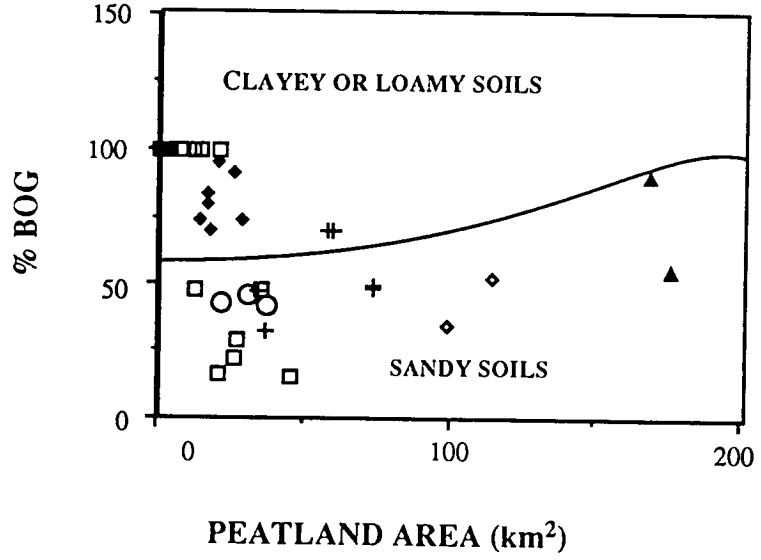


Figure 15b. The relationship of selected mire-complex types to soils in northern Minnesota. Peatlands dominated by bog landforms are generally located in areas of relatively impermeable clayey or loamy soils. Peatlands dominated by fens, however, are located in areas of permeable sands (Glaser in press).

The type 2 peatlands are nearly filled by several raised bogs that are separated by narrow water tracks. These peatlands are generally small (15-26 km^2) and consist mostly of bog (>75%). The bogs seldom have a conspicuous crest and generally have an eccentric cross-section. This peatland type corresponds to watershed III at North Black River (Glaser 1983a).

The type 3 peatlands have larger water tracks that originate near the upslope margin of the peatland. Runoff from the adjacent uplands drains directly into these water tracks, which drain downslope toward tributary streams. These peatlands are generally small (20-37 km^2), have nearly equal proportions of bog and fen (43: 57), and have a wide zone of mineral soil at the watershed crest. The bogs are widely separated by the water tracks, which generally lack the string-and-flark patterns. This peatland type corresponds to watershed II at North Black River in Minnesota (Glaser 1983a).

The type 4 peatlands have one huge water track that arises from the upslope margin of the peatland and splits downslope into 2 branches around a large raised bog. Several raised bogs may also occupy the lateral margins of the water track. These peatlands are very large (@100 km^2) and range from 34 to 54 % bog. This peatland type corresponds to the largest watersheds in the Myrtle Lake (Heinselman 1970) and North Black River (Glaser 1983a) peatlands in Minnesota.

The type 5 peatlands are distinguished by the concentration of raised bogs near the crest of the watershed, with broad water tracks downslope. One of these peatland types is small (37 km^2), but the others are intermediate in size (58-79 km^2), and the dimensions of several nearly completely overlap. Most of these peatlands have nearly equal proportions of bog and fen, but several are predominantly bog (70%).

The remaining discontinuous mire complexes consist of patterned fens (type 6;) and spring fens (type 7). These complexes lack raised bogs but differ greatly in size. The patterned fens range from the small (<1 km^2) to the huge patterned fens (> 20 km^2) in the three target areas (>60 km^2; Fig. 8). The spring fens, in contrast, are generally smaller

(0.3 - 15 km^2) although their watershed boundaries are somewhat arbitrary to define. In regions with discontinuous permafrost spring fens still produce the same general landform patterns except that the forested areas are pocketed by thermokarst collapse scars.

The continuous mire-complex types are restricted to the level terrain of the three target areas, where peat nearly covers the regional landscape. The semi-circular bogs of type 8 are situated along the linear beach ridges of Glacial Lake Agassiz, with their convex margin facing upslope. These bogs are associated with patterned water tracks, which split into 2 branches around the bog margin. These mire complex types are fairly common and superficially resemble types 4 and 10. The type 8 peatlands, however, are smaller (<36 km^2) and are predominantly fen (>50%).

The large bog complexes (type 9) of the Red Lake peatland in Minnesota have previously been described by Glaser *et al.* (1981). These complexes may cover more than 160 km^2 and largely consist of bog (55-90%). The bogs are divided into streamlined lobes and islands by water tracks that arise near the bog crest. This complex type is the most common peat landform in the Hudson Bay lowlands (Glaser 1987a). In areas with discontinuous permafrost the bogs are more finely dissected by water tracks but the same basic pattern prevails. Smaller bog complexes exhibit similar patterns but can be better placed in other peatland types on the basis of size.

The western water track (type 10) at Red Lake is also distinguished by its great size (>160 km^2) and the almost complete absence of bogs in the watershed (Fig. 10). Unlike the type 4 peatlands the western water track is surrounded by a vast belt of swamp forests, which grade downslope into linear fingers of forest and streamlined tree islands. In the Albany River region this complex type consists of featureless swamp forests that arise downslope from paludified moraines.

The Glacial Lake Agassiz region also contains several peat mounds that are dissected by spring-fen channels (type 5). These mounds are restricted to the Lost River peatland region

and are surrounded by large areas of peatland. The mounds range in size from 0.3 to 2.3 km^2.

4.1.4. Morphometry of Island Landforms

Streamlined bog islands are found in all three target areas, wherever fen water tracks completely surround raised bogs. The bog islands have rounded heads and long tapering tails oriented parallel to the direction of flow (Fig. 16). Approximately 40 of these islands were selected for morphometric analysis according to the methods devised by Baker (1978). The islands are located in the Red Lake peatland of northern Minnesota and the Pigeon River peatlands east of Lake Winnipeg. There is a high correlation between the length versus area, the width versus area, and length versus width of these islands. Power curve fitting of these data yields the empirical relationships

$$L = 1.64A^{0.47} \quad (R = 0.93) \qquad (1)$$

$$W = 0.73A^{0.46} \quad (R = 0.98) \qquad (2)$$

$$W = 0.43L^{0.85} \quad (R = 0.92) \qquad (3)$$

where L = length, W = width, and A = area of the islands. The quantitative correspondence of these islands to an idealized airfoil or streamlined strut was determined by calculating their average length-to-width ratio and by their average K factor, which defines a lemniscate loop (Baker 1978; Komar 1983, 1984). The average length-to-width ratio of these peat islands is 2.5, and the average K factor is 2.9.

4.2. Vegetation and Water Chemistry

4.2.1. Bog and Fen

Northern peatlands have traditionally been separated into bog and fen on the basis of their 1) peat landforms, 2) indicator species, 3) water chemistry, and 4) inferred hydrology (Fig. 1). Raised bogs can always be identified in Minnesota by their forested crest, acid

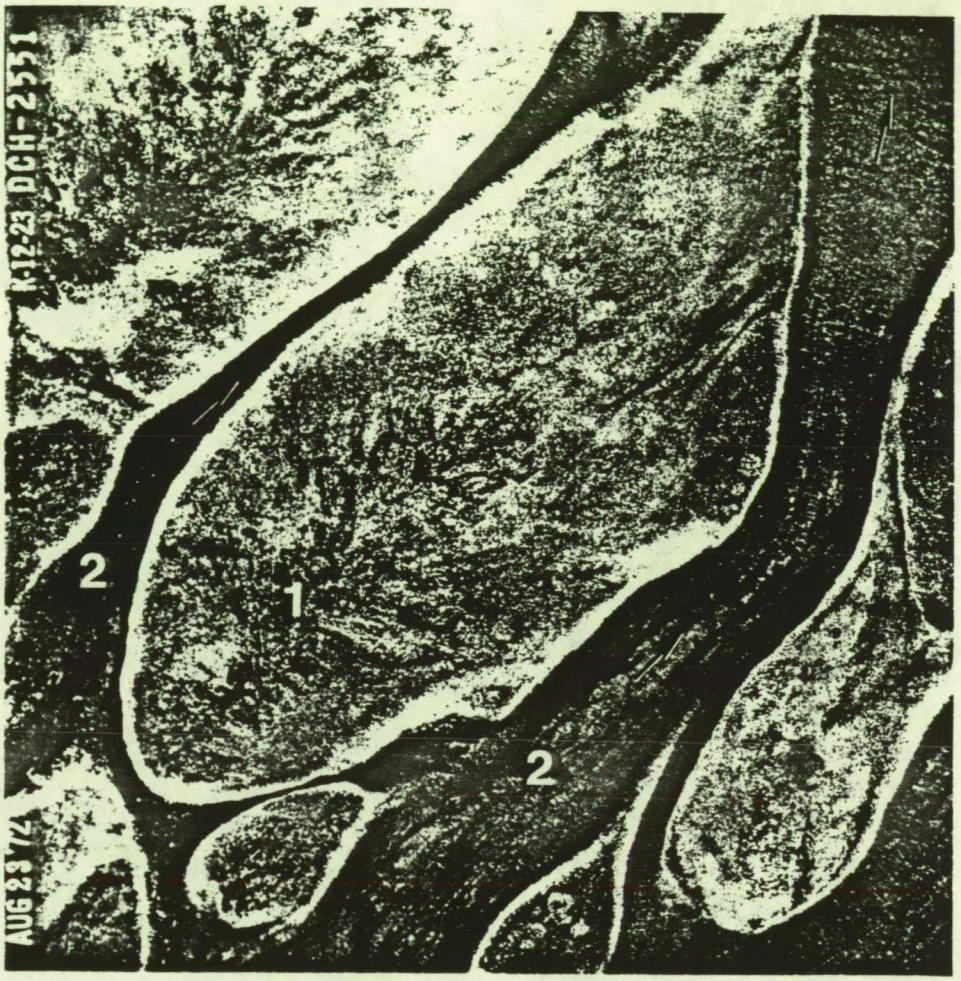


Figure 16. Streamlined bog islands from the Red Lake peatland, northern Minnesota. The large bog island in the center of the photo has a forested crest (1) and a streamlined margin that is trimmed by fen water tracks (2). The direction of flow in the water track is indicated by the arrows. The photo covers an area over 2.6 km broad.

waters (pH <4.2; Ca concentration <2 mg l^{-1}), and absence of fen indicator species. Farther north the forested crest grades into a nonforested plain in which the orientation of the pool networks indicates a raised profile in cross-section. Fens, in contrast, have concave landforms, less acid to alkaline waters (pH 4.2-7.2; Ca concentration 2-50 mg l^{-1}), and at least one indicator species present. These contrasting characteristics are linked to the hydrological properties of bogs and fens. The acid waters of bogs are maintained by internal sources of H^+ ions and by the absence of any significant external source for a base. The H^+ ions may be generated internally by the cation- exchange capacity of *Sphagnum* (Clymo 1963, 1967; Clymo and Hayward 1982) or by the release of organic acids through decomposition of *Sphagnum* peat (Gorham *et al.* 1984). The most important base in surface or ground waters, however, is carbonate, which is readily weathered from mineral soil by atmospheric precipitation (Drever 1982). Carbonate has a low concentration in bog waters because 1) the surface of the bog is raised above the flood level of runoff draining from the adjacent uplands, and 2) groundwater cannot move through the dense accumulation of bog peat. Thus bogs are believed to be *ombrotrophic* or rain-nourished, in contrast to fens, which are *minerotrophic* and receive at least some water that has percolated through mineral soil. The hydrogeological work in the Lost River peatland, however, disputes this commonly held belief. Analysis of Landsat imagery indicates that the fen vegetation in these large peat basins is controlled by the location of regional seepage faces for groundwater.

4.2.2. Raised Bogs

The ombrotrophic flora in the Glacial Lake Agassiz region contains less than 20 species of vascular plants (Table1). All of these species can also be found in fens, so bogs are distinguished by the **absence** of fen indicator species. The two best developed vegetation types (noda) on raised bogs are the *Carex trisperma - Vaccinium vitis-idaea* nodum in densely forested stands and the *Carex oligosperma* nodum on nonforested lawns (Glaser *et*

TABLE 1

LANDFORM	SURFACE FEATURE	COVER TYPE	CHEMISTRY	AREA
I. RAISED BOG				
1. FORESTED	FORESTED CREST	*PICEA/SPHAGNUM*	BOG	1,2
	NONFORESTED LAWN	*CAREX/SPHAGNUM*	BOG	1,2
2. NONFORESTED	POOLS	*NUPHAR*	BOG	2
	HOLLOWS	*SCIRPUS/SPHAGNUM*	BOG	2
	HUMMOCKS	ERICACEAE/*CLADONIA*	BOG	2
3. PEAT PLATEAUS	FORESTED HUMMOCKS	*PICEA/CLADONIA*	BOG	3
	NONFORESTED HOLLOWS	ERICACEAE/*SPHAGNUM*	BOG/FEN	3
II. SEDGE FENS				
1. WATER TRACKS	LINEAR POOL/RIDGE NETWORKS	*CAREX/SCORPIDIUM*	POOR-RICH FEN	1,2,3
2. RETICULATE FENS	RETICULATE POOL-RIDGE NETWORKS	*SCIRPUS/CAREX*	EXTREMELY RICH FEN	2,3
3. SPRING-FEN CHANNEL	ANASTOMOSING NETWORKS OF CHANNELS	*SCIRPUS/CAREX*	EXTREMELY RICH FEN	1,2,3
III. BOG COMPLEXES				
1. BOGS/WATERTRACKS	NARROW WATER TRACKS STREAMLINED BOG LOBES AND BOG ISLANDS	AS ABOVE	BOG-FEN	1,2,3

al. 1981). Most of the bog flora occurs on both lawns and forested stands, but *Carex trisperma, Vaccinium vitis-idaea, Gaultheria hispidula,* and *Smilacina trifolia* are generally restricted to forested stands, whereas *Carex oligosperma* is most common on lawns.

The stands of radiating forest generally consist of small trees of *Picea mariana* (<10 m tall) with occasional trees of *Larix laricina.* The trees are largest near the crest and gradually become smaller and more clumped downslope as the radiating lines of forest are more widely separated by nonforested bog drains. The lawns are dominated by *Carex oligosperma* , although small layered clumps of *Larix* and *Picea* are usually present. The ground layer consists of a continuous layer of *Sphagnum,* which forms easily compressible hummocks and ill-defined hollows.

In burned areas *Carex oligosperma* becomes dominant, and the assemblage assumes the character of a nonforested lawn. However, where the water table has been artificially lowered by drainage ditches *Carex oligosperma* does not colonize the burned area, which instead is dominated by a luxuriant growth of *Sphagnum* along with bog ericads, especially *Chamaedaphne calyculata..*

A rare vegetation type in Minnesota is the *Sphagnum cuspidatum* hollow (schlenke of northern European authors) that occur only near the bog crests at North Black River, Myrtle Lake, and Sturgeon River. The wetter moss carpet in these hollows contains a rare bog assemblage in Minnesota that includes *Carex limosa, Scheuchzeria palustris, Rhynchospora alba,* and *Utricularia cornuta.* These species are generally absent from most ombrotrophic sites in Minnesota, where the fluctuating water table may drop as much as 70-100 cm below the surface during a dry period.

With increasing pH and Ca concentration a number of minerotrophic indicator species appear on the *Sphagnum* lawns, representing a subtle change from ombrotrophic bog to minerotrophic poor fen. *Carex aquatilis* is the most common of these poor-fen indicators, followed by *Carex rostrata, C. chordorrhiza,* and *C. lasiocarpa.* Except for these indicator species the poor-fen relevés are almost indistinguishable from those of ombrotrophic bog.

The Albany River area contains the same forested and lawn vegetation types as those found in Minnesota. These noda contain virtually the same species of vascular plants although the lichen cover is more important in the northern peatlands. The northern bogs contain 3 additional vegetation types that are restricted to different landform patterns. The nonforested bog plains are marked by large pools that contain *Nuphar variegatum. Menyanthes trifoliata* is also present in pools containing typical bog waters, although elsewhere in North America this species is restricted to minerotrophic fens. Mud-bottom communities are well-developed in depressions that contain a distinct assemblage of species including *Rhynchospora alba, Utricularia cornuta, Carex limosa, Sceuchzeria palustris,* and a continuous carpet of bryophytes including *Sphagnum rubellum.* The nonforested bog plain also contains hummock communities dominated by ericaceous shrubs including *Kalmia angustifolia, Chamaedaphne calyculata,* and *Ledum groenlandicum* and a high cover of lichens. The greater microtopography of the bog surface supports the richest bog flora and most diverse bog vegetation within the three target areas. However, the most diverse bog vegetation and richest bog floras occur in the Maritime Provinces of eastern Canada.

The peat plateaus of the Hay River area contain very simple vegetation patterns and an exceptionally impoverished flora. The plateaus contain 2 vegetation types that are characterized by only a few species. The raised platforms underlain by permafrost are forested with stands of *Picea mariana* with occasional *Pinus banksiana,* and *Larix laricina.* The understory contains mostly ericaceous shrubs including *Ledum decumbens, L. groenlandicum, Chamaedaphne calyculata,* and *Andromeda glaucophylla* and abundant lichens. Depressions formed by thermokarst are usually carpeted by a continuous mat of *Sphagnum rubellum* and other bryophytes with a sparse cover of vascular plants. These hollows often contain minerotrophic waters.

4.2.3. Water Tracks and Spring Fens

The fen vegetation in these target areas is distinguished by 1) richer species assemblages, 2) the presence of minerotrophic fen indicators, and 3) the low representation of *Sphagnum* relative to the Amblystigeaceae mosses (Table 2). The indicator species are related to different ranges in water chemistry, although the indicators are most common in nonforested stands. Each of the different landform types is distinguished by a characteristic species assemblage, which can be identified as noda. These noda are actually reference points along a continuous gradient of vegetation change.

Spring-Fen Channels (*Scirpus hudsonianus-Cladium mariscoides* nodum)

The spring-fen channels are characterized by the *Scirpus hudsonianus-Cladium mariscoides nodum* (Glaser *et al.*, in press). These nonforested channels are dominated by sedges, the most important of which are *Scirpus cespitosus, Cladium mariscoides, Carex lasiocarpa,* and *C. exilis*. Also present are *Carex limosa, C. livida, Scirpus hudsonianus*, and *Rhynchospora alba*. The very alkaline waters (pH >6.8; Ca concentration >20 mg l^{-1}) in these channels are associated with a number of extremely-rich fen indicators including *Muhlenbergia glomerata, Cladium mariscoides, Parnassia palustris,* and *Thuja occidentalis*. The channels have standing water and scattered tussocks of sedges, which are slightly raised above the water level.

Flarks (*Triglochin maritima-Drosera intermedia* nodum)

The flarks are variable with respect to their area and depth of standing water. In the wettest locations *Triglochin maritima, Utricularia minor, Drosera intermedia, D. anglica,* and *D. linearis* are usually present (Glaser *et al.* 1981). The drier flarks usually lack these species. All flarks, however, are dominated by sedges including *Carex lasiocarpa, C. limosa, C. livida, C. chordorrhiza, Rhynchospora alba,* and *Menyanthes trifoliata*. The

relative abundance of these species changes with respect to water level and water chemistry. The flarks of pristine water tracks also contain several rare plants, which are restricted to fens in undisturbed locations.

Strings (*Carex cephalantha-Potentilla fruticosa* nodum)

Strings are very variable across the target areas. They are best developed in water tracks that have been ditched, whereas they are barely perceptible above the water level in the most pristine water tracks. Strings are also impossible to define in certain areas with small and shallow flarks. Strings are generally dominated by *Betula pumila* var. *glandulifera, Potentilla fruticosa, Salix pedicellaris* var. *hypoglauca, Carex diandra, C. cephalantha, Thelypteris palustris* var. *pubescens*, and *Viola pallens* var. *mackloskeyi.* In the wettest water tracks, however, strings also have sedges, such as *Carex lasiocarpa* and *C. chordorrhiza.*

Featureless water tracks (*Carex limosa - C. lasiocarpa* nodum)

Most water tracks have nonforested lawns that lack oriented pools. These sedge lawns are dominated by *Carex lasiocarpa* and *Rhynchospora alba,* with *Carex limosa, C. chordorrhiza,* and *Betula pumila* var. *glandulifera.* These sedge lawns are very similar to the flark nodum but lack the more aquatic species, such as *Drosera anglica, D. linearis, Utricularia minor,* and *Triglochin maritima.* Probably the most notable species absent from these featureless water tracks is *Carex livida,* which is virtually restricted to flarks and spring-fen channels in Minnesota. The featureless water tracks usually have standing water but there may be a continuous carpet of mosses including various Sphagna.

Forested Fingers (*Larix laricina-Carex chordorrhiza* nodum)

The margins of water tracks are often fringed by fingers of forest that extend out into the track and are dominated by *Larix laricina* with *Picea mariana.* The understory of these stands is dominated by *Carex chordorrhiza, C. lasiocarpa, C. leptalea, Betula pumila* var.

FOLDOUT FRAME /.

TABLE 2.

	SPRING-FEN CHANNELS (n =4)		FLARKS (n=26)		FEATURELESS WATER TRACKS (n=15)		STRINGS (n=7)		FOREST FINGERS (n=3)		TREE ISLANDS (n=4)		SPRING-FEN FORESTS (n=3)	
pH	6.6 - 7.6		4.8 - 7.4		4.2 - 7.1		6.2 - 7.2		4.8 - 6		6.4 - 7.2		6.8 - 7.2	
Ca concen. mg/l	55.9 - 98.5		2.0 - 56.5		1.5 - 30.4		2.1 - 65.8		1.5 - 11.1		13 - 65.9		30.7 - 45.6	
K conc.	44 - 64		22 - 149		26 - 181		20 - 129		42 - 129		20 - 128		21 - 35	
	FREQ.	COVER	FREQ.	COVER	FREQ.	COVER	FREQ.	COVER	FREQ.	COVER	FREQ.	COVER	FREQ.	COVER
Aster junciformis	0.75	+	-	-	-	-	-	+	-	-	-	-	-	-
Thuja occidentalis	100	+	0.11	+	-	-	0.14	2	-	-	0.75	+	-	-
Carex exilis	0.25	2	0.19	2	-	-	-	-	-	-	-	-	-	-
Cladium mariscoides	0.75	+	-	-	-	-	-	-	-	-	-	-	-	-
Parnassia palustris	100	+	0.15	+	-	-	0.14	+	-	-	-	-	-	-
Lobelia kalmii	100	+	0.26	+	-	-	0.43	+	-	-	-	-	-	-
Scirpus cespitosus	100	2	0.3	2	-	-	-	-	-	-	-	-	-	-
Drosera anglica	0.5	+	0.35	1	0.07	+	-	-	-	-	-	-	-	-
Drosera linearis	-	-	0.21	1	0.07	1	-	-	-	-	-	-	-	-
Utricularia minor	-	-	0.21	+	-	-	-	-	-	-	-	-	-	-
Triglochin maritima	0.5	-	0.41	+	+	0.13	0.14	+	-	-	0.25	+	-	-
Carex livida	0.5	+	0.9	1	0.2	+	0.14	+	-	-	-	-	-	-
Carex limosa	1	+	0.79	2	0.87	1	0.29	+	0.67	1	-	-	-	-
Menyanthes trifoliata	0.75	+	0.9	1	0.73	1	0.29	1	0.67	1	-	-	-	-
Rhyncospora alba	0.75	+	0.83	1	0.67	1	0.29	+	-	-	-	-	-	-
Utricularia intermedia	0.75	1	0.51	1	0.46	+	-	-	0.33	+	-	-	-	-
Eleocharis compressa	0.75	+	0.45	1	0.27	1	0.14	+	0.33	+	0.5	+	-	-
Equisetum fluviatile	-	-	0.52	1	0.4	1	0.43	+	-	-	0.33	+	-	-
Carex lasiocarpa	0.75	2	0.97	2	1	3	0.86	2	1	2	0.25	1	-	-
Betula pumila var. glandulifera	1	+	0.56	+	0.93	1	0.71	3	1	2	1	1	-	-
Salix pedicellaris var. hypoglauca	0.25	+	0.14	+	0.47	+	0.71	+	0.67	1	0.5	+	-	-
Andromeda glaucophylla	0.5	+	0.79	1	1	1	0.71	1	1	1	0.75	1	0.33	+
Drosera rotundifolia	0.25	+	0.34	+	0.53	+	0.43	+	0.66	+	0.75	+	0.66	+
Sarracenia purpurea	1	+	0.69	+	0.8	+	0.71	+	0.66	+	0.75	+	1	+
Carex chordorrhiza	-	-	0.82	1	0.93	1	0.71	3	1	1	0.5	1	0.33	+
Scheuchzeria palustris	0.25	+	0.82	1	0.53	1	0.53	+	0.33	+	-	-	-	-
Drosera intermedia	0.25	+	0.45	1	0.27	1	-	-	-	-	-	-	-	-
Kalmia polifolia	-	-	0.21	+	0.67	+	-	-	0.66	1	-	-	-	-
Chamaedaphne calyculata	-	-	0.41	1	0.8	1	0.29	1	1	2	0.75	1	0.66	+
Vaccinium oxycoccos	0.25	+	0.52	+	0.73	1	0.43	+	1	1	1	+	0.66	+
Larix laricina	0.75	1	0.28	1	0.47	1	0.56	1	1	4	1	4	-	-
Picea mariana	0.25	+	0.17	1	0.4	1	0.14	+	0.66	2	0.75	2	1	5
Smilacina trifolia	-	-	0.17	+	0.33	1	-	-	0.66	+	0.5	1	0.66	1
Carex paupercula	-	-	0.03	+	0.27	1	0.14	+	-	-	0.5	+	0.66	+
Ledum groenlandicum	-	-	0.07	+	0.27	+	0.14	+	1	+	1	2	1	3
Carex diandra	-	-	0.03	+	-	-	0.57	+	0.33	+	-	-	-	-
Thelypteris palustris var. pubescer	-	-	-	-	-	-	0.71	1	-	-	0.25	+	-	-
Viola pallens var. macklosheyi	-	-	-	-	-	-	0.57	+	0.33	+	0.25	+	-	-
Bromus ciliatus														
Agrostis scabra	0.25	+	0.1	+	-	-	0.43	+	-	-	-	-	-	-
Potentilla palustris	-	-	0.1	+	0.13	+	0.57	+	0.33	+	1	1	-	-
Typha latifolia	0.75	1	-	-	-	-	0.29	1	0.33	2	0.75	1	-	-
Carex leptalea	-	-	0.03	+	-	-	0.57	+	0.33	+	0.5	+	1	+
Galium labradoricum	-	-	0.07	+	0.07	+	0.57	+	-	-	1	+	0.33	+
Carex tenuiflora	-	-	-	-	0.07	+	0.14	+	1	+	0.5	+	0.67	+
Carex trisperma	-	-	-	-	-	-	-	-	-	-	0.5	+	0.67	2
Lysimachia thrysiflora	-	-	-	-	-	-	-	-	0.33	2	0.75	+	-	-
Vaccinium vitis-idaea	-	-	-	-	-	-	-	-	-	-	0.25	+	1	1
Pyrola secunda var. obtusata	-	-	-	-	-	-	0.29	+	-	-	0.5	+	0.33	+
Rumex orbiculatus	-	-	-	-	-	-	-	-	-	-	0.75	+	0.33	+
Dryopteris cristata	-	-	-	-	-	-	-	-	-	-	0.5	+	0.33	+
Carex disperma	-	-	-	-	-	-	-	-	-	-	0.75	+		
Caltha palustris	-	-	-	-	-	-	-	-	-	-	0.5	+	0.33	+
Cornus stolonifera	-	-	-	-	-	-	-	-	-	-	0.5	+		
Carex gynocrates	-	-	-	-	-	-	-	-	-	-	0.25	1		
Cornus canadensis	-	-	-	-	-	-	-	-	-	-	0.75	1	-	-
Gaultheria hispidula	-	-	-	-	0.07	+	-	-	-	-	0.5	+	0.33	+
Scirpus acutus	0.5	2	-	-	-	-	0.14	+	-	-	0.25	+	-	-
Habenaria clavellata	0.25	+	-	-	-	-	-	-	-	-	-	-	-	-
Scirpus hudsonianus	0.25	+	0.13	1	0.07	+	0.29	+	-	-	-	-	-	-
Potentilla fruticosa	0.5	+	-	-	-	-	0.14	+	-	-	-	-	-	-

glandulifera, Ledum groenlandicum, and *Chamaedaphne calyculata.* The forest canopy in these stands is not continuous, and the forest floor consists of a continuous carpet of *Sphagnum,* with high hummocks around the base of the trees and low, moist depressions.

Tree Islands (*Carex pseudocyperus-Aronia melanocarpa* nodum)

Water tracks may have small streamlined tree "islands." These islands are dominated by *Larix laricina* associated with *Picea mariana* and occasionally *Abies balsamea.* The islands are floristically similar to the forested finger nodum but are generally much richer in species. *Carex pseudo-cyperus* and *Aronia melanocarpa* are consistently present, along with *Betula pumila* var. *glandulifera, Ledum groenlandicum, Vaccinium oxycoccos, Potentilla palustris, Galium labradoricum* and *Lysimachia thrysiflora. Carex lasiocarpa* and *C. chordorrhiza* , however, are generally absent. The tree islands consists of moss-covered hummocks around the base of the trees and water-filled depressions.

Spring-Fen Forest (*Picea mariana- Carex gynocrates* nodum)

The spring-fen forests are dominated by *Picea mariana* but also contain *Larix laricina, Abies balsamea,* and *Thuja occidentalis. Carex gynocrates* is consistently present in the understory with *Smilacina trifolia, Carex paupercula, Ledum groenlandicum, Carex trisperma,* and *Vaccinium vitis-idaea.* The spring-fen forests usually have a nearly continuous canopy and a continuous carpet of moss on the substrate. Standing water is unusual in these stands, but the water table is usually close to the surface.

4.2.4. Water Chemistry

The water chemistry from the vegetation samples may be divided into 2 major classes on the basis of pH and calcium concentration. The ombrotrophic bog samples have a pH below 4.2 and calcium concentrations below 2 mg l^{-1}, whereas the minerotrophic fen samples have values above this level.

The bog samples have very narrow ranges for pH (3.7-4.1) and calcium concentration (0.6-2.0 mg l^{-1}). A few bogs have unexpectedly high concentrations of Ca but otherwise seem to be ombrotrophic. These samples were taken from pits, because standing water was not present at the surface, and they may represent complex exchanges with the subsurface peat. The water chemistry of the bog samples does not differentiate among the various types of vegetation-landform on bogs, except that absorbance readings tend to be lower at the bog crest, indicating higher rates of flow.

Extremely poor fens (*sensu* Sjörs 1950) are distinguished by a pH of 3.8-5.0. In the target areas these fens generally exhibit the most sensitive floristic response to small changes in water chemistry. A group of poor fens that have bog-like vegetation is characterized by a pH of 4.1-4.6 and Ca concentrations of 2.2-5.5 mg l^{-1}. These samples were taken from relevés containing one or more minerotrophic indicators (*sensu* Sjörs 1963, 1983; Glaser *et al* 1981; Wheeler *et al.* 1983) with low cover values.

The other group of poor fens recognized by Sjörs (1950) has considerable overlap in pH and is characterized by Heinselman (1970) as weakly minerotrophic, with a pH of 4.3 to 5.8 and Ca concentrations of 3-10 mg l^{-1}. The samples that fall within this range were taken from relevés whose vegetation was very similar to that of the water tracks. These samples had a pH of 4.1-5.9 and Ca concentrations of 0.9-13.0 mg l^{-1}. Many of the small patterned fens from northeastern Minnesota fall into this class, along with water tracks from the Albany River region.

The transitional rich fens of Sjörs (1950) or minerotrophic class of Heinselman (1970) is characterized by a pH of 5.8 to 7 and Ca concentrations of 10-25 mg l^{-1}. The water samples from northern Minnesota that fall into this class have a pH of 5.9-6.8 and Ca concentrations of 10-32 mg l^{-1}. Other samples, however, are transitional to the poor-fen class and are difficult to categorize with certainty.

Extremely-rich fens, which Sjörs (1950) distinguishes as having a pH of 7 to about 8.5, are the only class of fen samples that are generally restricted to particular landform

units. Water samples from the spring fens have a pH of 6.8-7.4 and Ca concentrations of 20-45 mg l^{-1}. These landforms are common within the three target areas, although spring fen channels from the Albany River region exhibit slightly lower values for pH and Ca concentration. Only a few samples from patterned fens in Minnesota have values in the extremely rich fen range, but reticulate fens in the Albany River and Hay River areas consistently have a pH greater than 7.5. The chemistry of these fens seems to indicate groundwater discharge from the underlying calcareous till.

4.2.5. Environmental Gradients

The vegetation in patterned peatlands is closely related to landform type and water chemistry. This relationship is documented by Detrended Correspondence Analysis (DCA), a multivariate method for determining the underlying pattern within a large data set composed of many different variables (Hill 1979). The fen relevés from northern Minnesota, for example, are consistently grouped according to landform type and secondarily by water chemistry (Fig. 17). This close correspondence among the vegetation, landform, and water chemistry is surprising when the regional spacing of the samples is considered and when many relevés from disturbed peatlands in Minnesota are included.

The DCA ordination indicates that 2 environmental gradients control the composition of the vegetation. Most of the variation in the data set is expressed along axis 1, which corresponds closely to the moisture gradient. The driest forested stands are located on the right side of the ordination, whereas the wettest flarks are located on the left. The influence of water chemistry is indicated by axis 3, with poor fens positioned at the bottom and richer fens toward the top of the axis.

The effect of water chemistry on the relative abundance of the dominant mire species is best illustrated by direct gradient analysis (*sensu* Whittaker 1967). The major fen dominants attain their peak in abundance within specific ranges of water chemistry with the

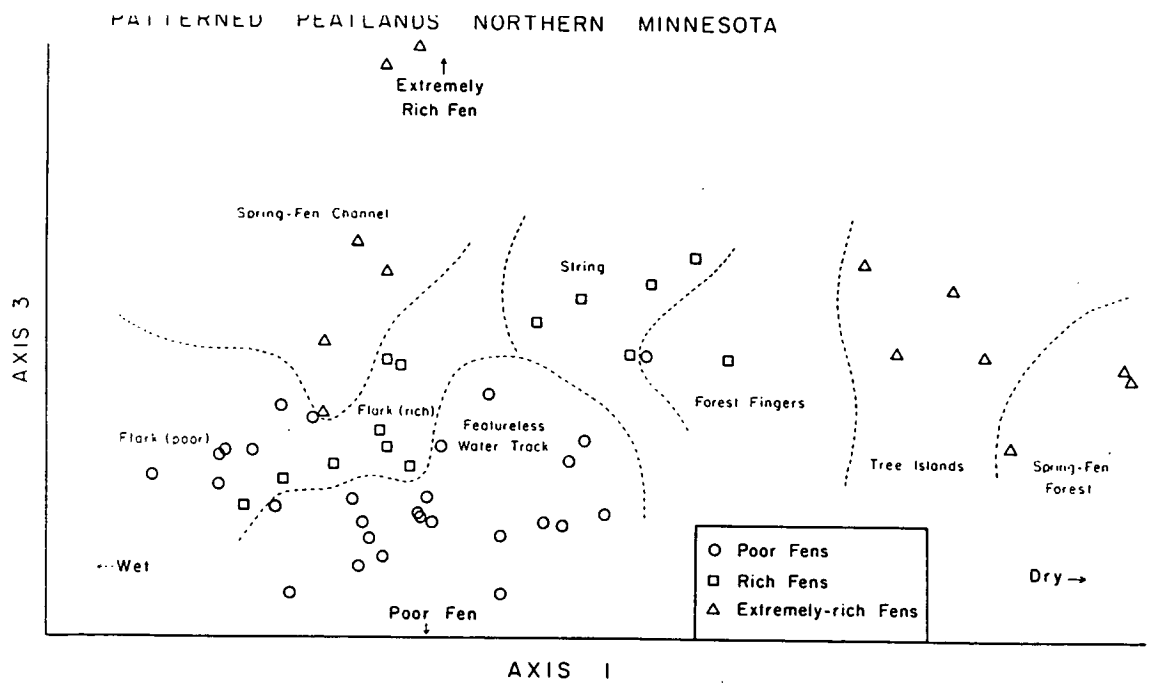
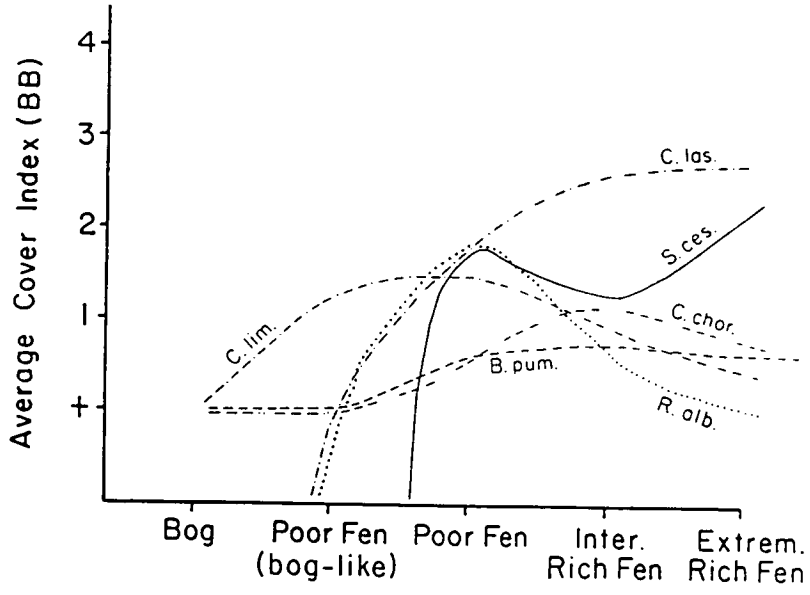


Figure 17. Ordination of fen vegetation by detrended correspondence analysis. The fen vegetation is separated into groups that correspond to landform type and water chemistry. The first ordination axis corresponds most closely to a moisture gradient with the wetter stands on the left and drier stands on the right. The third ordination axis corresponds to the chemical gradient, with the poor-fen waters below and extremely-rich fen waters above (Glaser 1987b, in press).



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Figure 18. Direct gradient analysis of the major vascular plant species along a chemical gradient. The average cover value (Braun-Blanquet index) of each species is plotted in relation to the water chemistry. The symbols for the Braun-Blanquet index are (+) sparsely present; (1) plentiful but low cover value; (2) very numerous, or covering at least 5% of the area; (3) very numerous or covering 25-50% of the area; (4) any number of individuals covering 50-75% of the area; (5) covering more than 75% of the area. The ranges in water chemistry are bog (pH <4.2; Ca concentration <2 mg l^{-1}); poor fen: bog-like (pH 4.1-4.6; Ca concentration 1.5-5.5 mg l^{-1}); poor fen: fen-like (pH 4.1-5.8; Ca concentration <10 mg l^{-1}); intermediate rich-fen (pH 5.8-6.7; Ca concentration 10-32 mg l^{-1}); extremely rich fen (pH >6.7; Ca concentration >30 mg l^{-1}) (Glaser 1987b, in press).

exception of *Scirpus cespitosus* , which has separate peaks in the poor-fen and extremely-rich fen range, and *Betula pumila* var. *glandulifera,* which has a fairly uniform distribution across the entire rich-fen range (Fig. 18). The direct gradient analysis of the major bog-fen species, however, demonstrates that many of these species are relatively insensitive to changes in water chemistry (Fig. 19). *Picea mariana* and bog ericads such as *Chamaedaphne calyculata* and *Ledum groenlandicum* have two 2 peaks in abundance at the opposite ends of the chemical gradient. These species apparently respond to the moisture gradient and become dominant on the driest landforms irrespective of the water chemistry. *Larix* , however, is more common in the fen range and is similar in behavior to *Betula pumila.*

Plant succession may also play an important role in determining the vegetation patterns in these peatlands. Two types of poor fen occur in northern Minnesota, with similar ranges in water chemistry and water levels but very different types of vegetation. One type occurs on the *Sphagnum* lawns and is almost indistinguishable from ombrotrophic bog vegetation, whereas the other type is very similar to that found in the more minerotrophic flarks and featureless water tracks. The major division between these two types of poor fen actually separates the overall peatland vegetation into two contrasting types much better than the more subtle floristic changes that occur at a pH of 4.2 and Ca concentration of 2 mg l^{-1}. These two types of poor fen seem to represent the opposing end products of development for bogs and fens.

The factor that best integrates the varying effect of water chemistry, moisture, and plant succession on the mire vegetation is the landform patterns. Direct gradient analysis indicates the degree to which different species attain dominance on different landform types, particularly the different types of poor fen (Fig. 20). Subtle changes in the form of these patterns also provides an important tool for interpreting the direction of plant succession and influence of the major environmental controls.

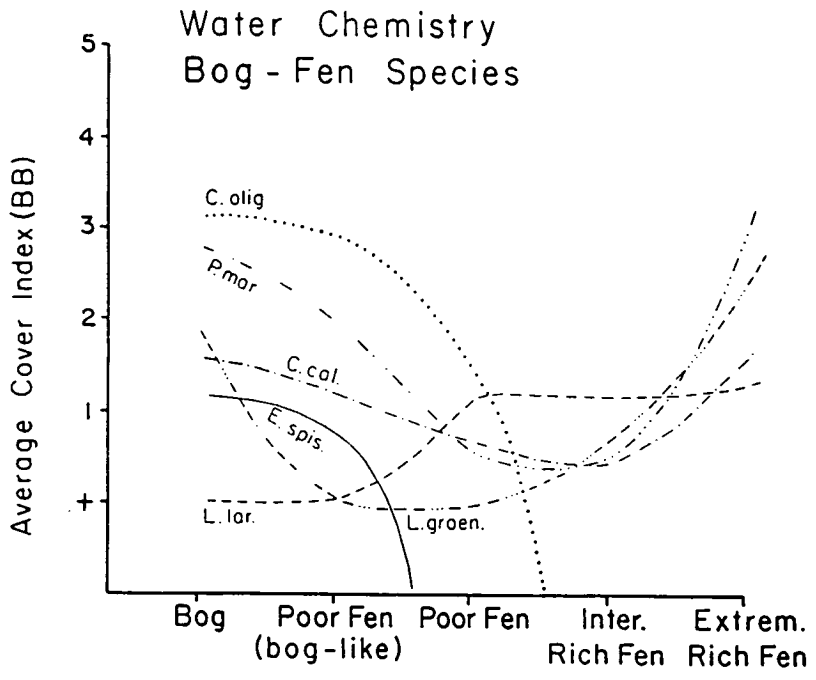


Figure 19. Direct gradient analysis of the major vascular plants in both bogs and fens. Dual peaks in abundance for various species may indicate that these species respond to a different environmental factor. See Figure 18 for the average cover values and ranges in water chemistry (Glaser 1987b, in press).

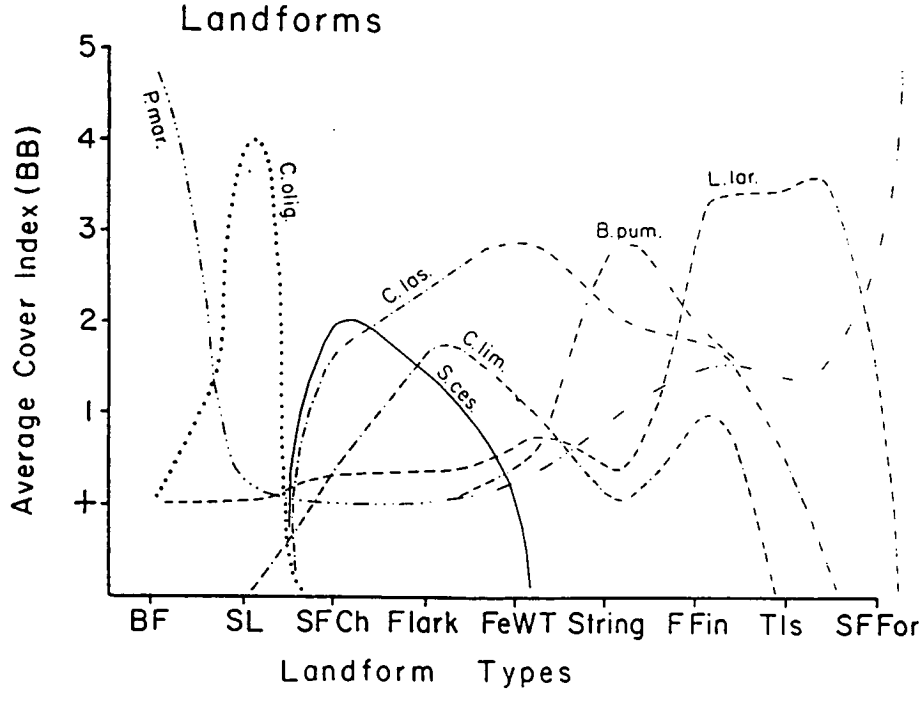
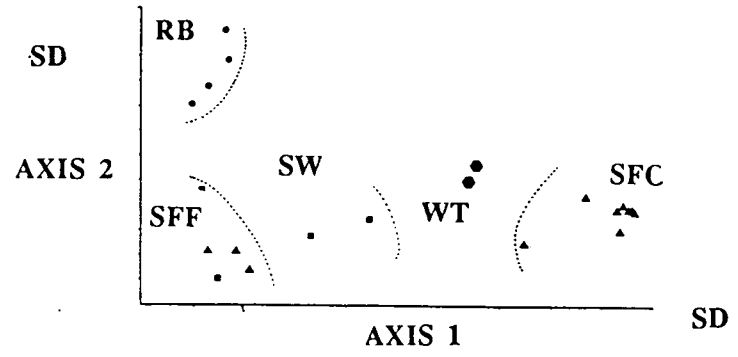


Figure 20. Direct gradient analysis of the major vascular plant species with respect to landform type. Each species reaches its peak abundance on a different landform type (Glaser *et al.* in press).

FIGURE 21A



KEY

RB: RAISED BOG

SFF: SPRING-FEN FOREST

SW: SWAMP FOREST

WT : WATER TRACK

SFC: SPRING-FEN CHANNEL

FIGURE 21B

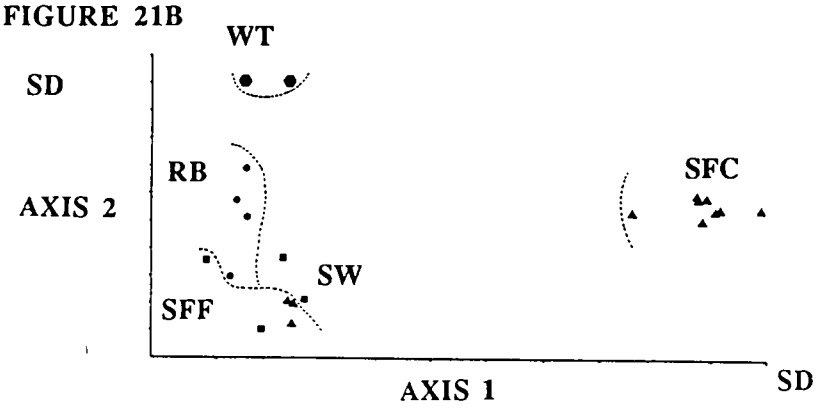


FIGURE 21C

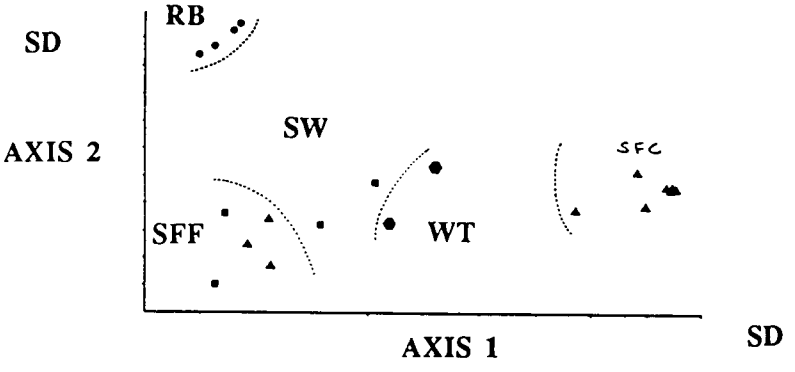


Figure 21 Detrended correspondence analysis of the vegetation relevés from Lost River. The 3 plots present ordinations for the vascular plant data (21a), the bryophyte data (21b), and the combined data set (21c). The water chemistry of the relevés is indicated by the symbols: circles (bog), hexagons (poor fen), squares (rich fen), and triangles (extremely rich fen). The eigenvalues for axis 1 are 0.738 (5a), 0.705 (5b), and 0.700 (5c). The eigenvalues for axis 2 are 0.205 (5a), 0.191 (5b), 0.188 (5c) (Glaser *et al.* in press).

Table 3

	Spring-Fen Channel								Spring-Fen Forest					Swamp Forest		Water Track		Raised Bog			
Relevé No.	107	111	112	113	114	115	109	110	108	116	117	118	119	122	120	121	123	190	191	124	125
pH	7.1	7.3	7.1	7	7.1	7	7	7.1	-	7.5	7	6.6	6.6	6.8	6.3	4.6	5.3	4	4	3.9	4.01
K ...	318	305	192	229	227	192	178	222	-	196	240	150	136	111	68	24	19	62	55	11	14
Ca	36	45	28	37	35	26	25	20	-	30	30	19	16	10	8	3	3	0.8	1.1	0.8	1.1
1. Muhlenbergia glomerata (a1)	+.2	+.2	+.2	+.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2. Typha latifolia	+.1	-	+.1	+.2	+.1	+.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Carex exilis	3.2	-	1.2	+.2	1.2	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4. Drosera anglica	+.2	+.2	+.2	-	+.1	+.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5. Scirpus cespitosus	4.4	4.2	4.3	3.2	3.3	4.4	3.2	3.3	-	-	-	-	-	-	-	-	-	-	-	-	-
6. Scirpus hudsonianus (a2,a3)	1.2	+.2	1.2	1.2	1.2	+.2	1.2	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-
7. Habenaria clavellata	+.1	-	+.2	-	+.1	+.2	-	+.1	-	-	-	-	-	-	-	-	-	-	-	-	-
8. Utricularia intermedia (a3)	+.2	-	1.2	1.2	1.2	+.2	-	+.2	-	-	-	-	-	1.2	-	-	+.2	-	-	-	-
9. Carex limosa	3.2	2.2	3.3	3.2	4.3	2.2	1.2	3.3	-	-	-	-	-	-	-	+.2	+.2	-	-	-	-
10. Rhynchospora alba	+.2	+.2	1.2	1.2	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Cladium mariscoides (a1)	+.2	1.2	2.2	2.2	2.3	2.2	-	3.2	-	-	-	-	-	-	-	-	-	-	-	-	-
12. Parnassia palustris (a1)	+.1	+.2	+.1	+.2	+.2	+.2	+.2	+.2	-	-	-	-	-	-	-	-	-	-	-	-	-
13. Eleocharis compressa (a)	+.2	+.2	1.2	+.2	+.2	1.2	-	+.2	-	-	-	-	-	+.2	-	-	-	-	-	-	-
14. Carex livida (a2)	+.1	+.2	1.2	+.2	+.1	+.1	-	+.2	-	-	-	-	-	-	-	-	-	-	-	-	-
15. Utricularia cornuta	-	+.2	+.2	+.2	+.2	+.2	-	+.1	-	-	-	-	-	-	-	-	-	-	-	-	-
16. Carex aquatilis (a)	-	-	+.1	-	-	1.2	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17. Phragmites communis (a)	-	-	+.2	-	+.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18. Thuja occidentalis (a1)	+.1	+.1	+.2	-	+.2	+.1	3.2	1.2	+.2	2.2	+.2	-	-	1.1	+.1	-	-	-	-	-	-
19. Carex lasiocarpa (a2)	2.2	3.2	2.2	2.2	1.2	2.2	2.2	2.2	-	-	-	-	-	1.2	-	4.3	4.4	-	-	-	-
20. Larix laricina	+.1	-	+.2	+.1	-	+.1	-	+.2	+.1	-	-	-	+.2	1.1	+.2	1.2	2.2	-	-	-	-
21. Menyanthes trifoliata (a3)	+.2	+.1	2.2	1.2	1.2	+.2	-	+.1	-	+.2	-	-	-	1.2	+.2	+.2	-	-	-	-	-
22. Sarracenia purpurea	1.2	1.2	1.2	1.2	+.1	-	1.2	1.2	+.2	1.2	+.2	+.2	-	+.2	+.2	+.2	+.2	-	-	-	-
23. Betula pumila var. glandulifera (a3)	-	+.2	-	+.1	+.2	+.2	1.2	1.2	-	-	-	-	-	2.1	2.2	-	+.2	-	-	-	-
24. Carex interior (a)	-	+.2	-	-	-	+.2	-	-	-	+.2	-	-	-	+.2	+.2	-	-	-	-	-	-
25. Rhamnus alnifolia (a1)	-	+.2	-	-	-	-	+.1	-	1.2	1.2	+.2	-	+.2	1.2	1.2	-	-	-	-	-	-
26. Carex leptalea (a2)	-	-	-	+.2	-	-	-	-	2.2	3.2	2.2	-	-	-	+.2	-	-	-	-	-	-
27. Coptis groenlandica	-	-	-	-	+.1	-	-	-	-	+.2	1.2	-	+.2	-	-	-	-	-	-	-	-
28. Andromeda glaucophylla	+.2	2.2	1.2	1.2	1.2	+.2	-	+.1	-	+.2	-	+.2	-	3.2	-	-	2.2	1.1	2.2	1.2	1.2
29. Drosera rotundifolia	+.1	+.2	+.2	+.1	+.2	+.2	+.2	-	+.2	+.2	+.2	r.1	-	+.2	-	+.2	+.2	-	-	+.2	+.2
30. Ledum groenlandicum	+.1	-	-	-	-	-	+.2	-	2.2	2.2	3.3	3.2	4.3	2.2	-	-	-	3.3	4.4	2.2	2.2
31. Vaccinium oxycoccos	-	+.2	+.2	+.2	+.2	-	+.2	-	+.2	+.2	+.2	+.2	1.2	1.2	+.2	1.2	+.2	2.2	2.2	1.2	1.2
32. Picea mariana	-	+.1	+.2	-	-	+.2	+.2	-	4.5	4.2	5.2	5.1	+.2	2.2	2.2	-	+.2	5.2	5.2	5.2	5.2
33. Lonicera villosa var. solonis	-	-	-	-	-	-	2.2	-	+.2	-	-	-	+.2	1.2	1.2	-	-	-	-	-	-
34. Equisetum fluviatile (a3)	-	-	-	-	-	-	+.1	-	-	-	-	-	-	1.2	1.2	1.2	1.1	-	-	-	-
35. Eriophorum viridi-carinatum (a2)	-	-	-	-	-	-	+.1	-	-	-	+.2	-	+.1	+.2	+.2	-	-	-	-	-	-
36. Galium labradoricum	-	-	-	-	-	-	-	+.1	+.1	+.2	-	-	-	+.2	-	-	-	-	-	-	-
37. Carex paupercula	-	-	-	-	-	-	-	-	1.2	+.2	+.2	+.2	+.2	1.2	1.2	-	-	-	-	-	-
38. Carex tenuiflora (a2)	-	-	-	-	-	-	-	-	+.2	-	-	+.2	+.2	+.2	+.2	-	+.2	-	-	-	-
39. Carex gynocrates (a1)	-	-	-	-	-	-	-	-	3.3	3.2	4.2	2.2	2.2	1.2	1.2	-	-	-	-	-	-
40. Trientalis borealis	-	-	-	-	-	-	-	-	-	+.2	+.2	-	+.2	+.2	-	-	-	-	-	-	-
41. Potentilla palustris (a)	-	-	-	-	-	-	-	-	-	+.2	-	-	-	1.2	+.2	-	+.2	-	-	-	-
42. Maianthemum canadense	-	-	-	-	-	-	-	-	-	-	-	+.2	+.2	+.2	+.2	-	-	-	-	-	-
43. Rubus pubescens	-	-	-	-	-	-	-	-	-	-	-	-	1.2	+.2	+.2	-	-	-	-	-	-
44. Carex chordorrhiza (a3)	-	-	-	-	-	-	-	-	-	-	-	-	-	3.2	2.2	-	3.2	-	-	-	-
45. Lysimachia thyrsiflora (a)	-	-	-	-	-	-	-	-	-	-	-	-	-	+.2	+.2	-	-	-	-	-	-
46. Smilacina trifolia	-	-	-	-	-	-	-	-	3.2	3.2	2.2	1.2	2.2	+.2	1.2	-	-	2.2	2.2	+.2	1.2
47. Vaccinium vitis-idaea	-	-	-	-	-	-	-	-	1.2	2.2	2.2	2.2	2.2	+.2	+.2	-	-	2.2	2.2	-	-
48. Carex trisperma	-	-	-	-	-	-	-	-	2.2	-	+.2	1.2	+.2	-	+.2	-	-	1.1	3.3	-	1.2
49. Chamaedaphne calyculata	-	-	-	-	-	-	-	-	+.2	+.2	+.2	+.2	1.2	+.2	1.2	1.2	1.2	2.2	2.2	+.2	2.2
50. Gaultheria hispidula	-	-	-	-	-	-	-	-	+.1	+.2	+.2	-	+.2	-	-	-	-	+.2	+.2	-	-
51. Vaccinium myrtilloides	-	-	-	-	-	-	-	-	-	+.2	+.2	+.2	-	-	+.2	-	-	+.1	3.3	-	-
52. Kalmia polifolia	-	-	-	-	-	-	-	-	-	-	+.2	-	-	+.2	+.2	+.2	-	3.3	1.2	3.2	2.2
53. Enophorum spissum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.2	2.2	2.2	3.2

Additional Species (releve no., cover, and sociability):

Drosera linearis (107, 1.2); Viola sp. (107, +.2; 114, +.1); Habenaria clavellata (107, +.1; 114, +.2; 116, +.2); Salix pedicellans var. hypoglauca (107,+.1); 122, 2.2, 121, +.2), Triglochin maritima (107, +.1, 111, +.2, 112, +.2, 115, +.1, 110, +.1, 122, 1.2); Carex prairea (111, +.2, 108, +.2, 122, +.2); Carex interior (111, +.2, 115, +.2, 116, +.2, 122, +.2, 120, +.2). Salix discolor (111, +.1); Salix semsima (111, 1.2, 112, +.2, 108, +.1); Salix candida (111, +.1, 122, +.1, 120, +.2, 117, +.1); Rubus acaulis (111, +.1, 116, +.1, 119, +.1, 122, +.2); Habenaria hyperborea (111, +.2, 109, +.1, 115, +.2); Carex capillaris (112, +.2, 116, +.2); Carex diandra (113, +.2); Myrica gale (113, +.1); Amelanchier humilis (113, +.1); Carex disperma (114, +.2); ukn. (114, +.1); Potentilla fruticosa (109, 3.2, 110, 2.2); Thelypteris palustris var. pubescens (110, +.1, 122, 1.2); Pyrola sp. (109, +.1); Linnea borealis (108, 1.2, 116, +.2); Cypripedium acuale (108, r.1); Mitella nuda (108, +.1, 116, +.1); Orchis rotundifolia (108, +.2, 116, +.2, 117, +.2); Habenaria obtusata (108, +.1); Ribes hudsonianum (108, +.1); Pyrola secunda (108, +.1, 119, +.2, 120, +.1); Epilobium leptophyllum (108, +.1); Campanula aparinoides (108, +.1, 120, +.2); Caltha palustris (108, +.2, 117, +.2, 118, +.2); Malaxis uniflora (116, +.2); Botrychium virginianum (116, +.2); Pyrola assarifolia (116, +.2, 120, +.1); Lonicera oblongata (116, +.2, 117, +.2); Cornus canadensis (117, +.2, 118, +.2); Listera cordata (117, +.1); cf. Calamagrostis (117, +.1); Chimaphila umbellata (118, r.1); Calamagrostis inexpansa (119, +.2); Salix bebbiana (119, +.2, 120, +.2); Alnus rugosa (122, 1.2); Salix gracilis (122, +.2); Osmunda cinamomea (120, +.2); Glyceria striata (120, +.2); Calopogon pulchellus (120, +.2), Calamagrostis canadensis (120, +.2); Eriophorum gracile (190, 2.2); Carex oligosperma (125, 2.2); Carex pauciflora (125, 2.2).

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Table 4

Relevé No.	Spring-Fen Channel								Spring-Fen Forest					Swamp Forest		Water Track		Raised Bog			
	107	111	112	113	114	115	109	110	108	116	117	118	119	122	120	121	123	190	191	124	125
54. Calliergon trifarium (a1,a2)	+	+	+	+	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
55. Campylium stellatum (a1,a2)	3	2	3	3	4	2	2	2	+	+	+	.	.	.	.	.	.	.	.	.	.
56. Cinclidium stygium (a1,a2)	+	.	+	+	.	+	.	.	+	+	.	.	.	+	+	.	.	.	.	.	.
57. Drepanocladus revolvens (a2)	+	1	1	2	3	2	2	1	+	+	.	.	.	.	.	.	+	.	.	.	.
58. Fissidens adiantoides	+	.	+	.	+	+	+	+	.	.	+	.	.	3	.	.	.	.	.	.	.
59. Hypnum lindbergii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
60. Moerckia hibernica	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.
61. Scorpidium scorpioides (a1,a2)	2	2	2	3	3	2	.	2	.	+	.	.	.	+	+	.	.	.	.	.	.
62. Aulacomnium palustre	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
63. Bryum pseudotriquetrum	.	+	+	+	+	1	.	+	2	+	+	+	.	+	+	+	2	+	.	+	+
64. Riccardia latifrons	.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.
65. Tomenthypnum nitens (a1,a2)	.	+	+	+	+	+	.	+	+	+	+	+	.	+	+	.	.	.	.	.	.
66. Lophocolea heterophylla	.	+	+	+	+	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.
67. Fissidens osmundoides	.	.	+	.	.	.	.	.	+	.	.	+	.	2	.	.	+	.	.	.	.
68. Campylium hispidulum	.	.	.	.	+	.	.	.	.	+	.	.	.	+	+	.	.	.	.	.	.
69. Campylium polygamum	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.
70. Dicranum undulatum	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.
71. Calliergon giganteum (a1,a2)	.	.	.	.	.	.	+	.	2	.	1	+	+	+	+	+	.	.	.	.	.
72. Calliergon richardsonii (a2)	.	.	.	.	.	.	.	.	+	1	.	.	.	3	+	.	.	.	.	.	.
73. Calypogeia integristipula	.	.	.	.	.	.	.	.	+	+	.	.	.	+	+	.	.	.	.	.	.
74. Dicranum flagellare	.	.	.	.	.	.	.	.	+	+	+	.	.	+	+	.	.	.	.	.	.
75. Dicranum montanum	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	+
76. Dicranum polysetum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
77. Hylocomnium splendens	.	.	.	.	.	.	.	.	+	2	2	1	.	.	.	.	.	.	.	.	.
78. Hypnum pratense	.	.	.	.	.	.	.	.	+	2	3	3	.	.	2	.	.	1	1	+	.
79. Lepidozia reptans	.	.	.	.	.	.	.	.	+	.	+	+	.	+	+	.	.	.	.	.	.
80. Plagiomnium ellipticum	.	.	.	.	.	.	.	.	+	1	.	.	.	+	.	.	.	.	.	.	.
81. Pleurozium schreberi	.	.	.	.	.	.	.	.	2	4	5	3	2	2	3	.	.	.	.	.	.
82. Polytrichum strictum	.	.	.	.	.	.	.	.	+	.	+	+	.	+	.	.	.	.	.	.	.
83. Ptilidium pulcherrimum	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	2	3	1	1	1	1
84. Ptilium crista-castrensis	.	.	.	.	.	.	.	.	+	1	+	+	.	.	.	.	.	+	+	+	+
85. Rhizomnium gracile	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.
86. Rhizomnium pseudopunctatum	.	.	.	.	.	.	.	.	+	+	.	+	+	.	.	.	.	.	.	.	.
87. Sphagnum angustifolium	.	.	.	.	.	.	.	.	2	3	2	2	2	2	2	1	3	3	3	4	3
88. Sphagnum fuscum	.	.	.	.	.	.	.	.	+	+	2	+	+	1	+	3	+	3	3	1	+
89. Sphagnum magellanicum	.	.	.	.	.	.	.	.	3	3	.	.	5	3	3	3	3	3	3	1	1
90. Sphagnum capillifolium	.	.	.	.	.	.	.	.	+	3	+	2	3	.	.	+	+	+	+	+	+
91. Sphagnum russowii	.	.	.	.	.	.	.	.	3	+	.	+	+	2	2	.	.	.	.	.	.
92. Sphagnum warnstorfii (a1,a2)	.	.	.	.	.	.	.	.	2	+	+	.	.	.	.	.	.	.	.	1	.
93. Tomenthypnum falcifolium (a3)	.	.	.	.	.	.	.	.	+	+	.	+	2	.	.	1	.	.	.	.	.
94. Callicladium haldanianum	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	.	.	.	.
95. Cephalozia connivens	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.
96. Mylia anomala	.	.	.	.	.	.	.	.	+	.	+	+	+	+	+	+	.	.	+	+	+
97. Calliergon stramineum	.	.	.	.	.	.	.	.	+	.	.	.	+	+	+	+	.	.	+	+	+

Additional Species (releve no. and cover)

Riccardia palmata (107: +; 112: +; 108: +); Scorpidium turgescens (107: +); Catoscopium nigritum (112: +); Cephalozia pleniceps (114: +; 108: +); Pterigynandrum filiforme (114:+); Aneura pinguis (115:+; 121:+; 123: +); Sphagnum warnstorfii (109: 2); Geocalyx graveolens (109:+; 116:+); Campylium chrysophyllum (110: +); Bazzania trilobata (108: +; 117: +); Blepharostoma trichophyllum (108: +; 121:+); Brachythecium curtum (108: +; 116:+); B. salebrosum (108: +; 117: +; 120:+); Calliergon aftonianum (108: +; 120:+; 121: +); Campylium radicale (108:+), Drepanocladus uncinatus (108: +; 121: +; 123: +), Eurhynchium pulchellum (108: +; 116:+); Helodium blandowii (108: +; 121: +); Hypnum fertile (108: +; 116: +); Plagiochila asplenoides (110:+; 116: +); Plagiomnium cuspidatum (108:+); Plagiothecium denticutatum (108: +); Pohlia nutans (108: +; 116: +); Pylaisiella polyantha (108: +; 116: +; 121: +); Rhynchostegium serrulatum (108: +); Rhytidiadelphus triquetrus (108: +; 116: +); Sphagnum squarrosum (108: +; 120:+; 121: +); Tetraphis pellucida (108: +; 118:+); Amblystegium serpens (116: +); Thuidium delicutatum (116: 2); Dicranum scoparium (116: +); Fruttania eborascensis (116: +); Isopterygium sp. (116: +); Lophocolea minor (116: +); Lophozia rutheana (116: +; 117: +; 120: +); Myurella julacea (116: +); Orthotrichum sp. (116: +); Radula complanata (116: +); Riccardia multifida (116: +); Sphagnum centrale (116: +; 123: +); Sphagnum jensenii (116: +); Thuidium recognitum (116: +; 120: +); Sphagnum wuttianum (118: 1); Brachythecium campestre (118: +; 121: +; 120: +); Brachythecium rivulare (118: +); Hertzogiella turfacea (118: +); Isopterygiopsis muelleriana (118:+); Marchantia polymorpha (118: +); Platygyrium repens (118: +), Hypnum pratense (119: +); Ahastrophytum minutum (122: +); Calypogea sphagnicola (122: +); Cephaloziella elachista (122: +; 123: +; 125: +); Cephaloziella hampeana (122: +); Chiloscyphus pallescens (122: +); Drepanocladus exannulatus (122: +); D. fluitans (122: +; 123: +); Gymnocolea inflata (122: +); Pohlia sp. (122: +; 123: +; 190: +; 124: +); Scapania paludicola (122: +; 121: +; 123: +); Sphagnum fallax (122: 2; 124: +); Sphagnum flexuosum (122: +; 125: +); Sphagnum subsecundum (122:+; 123:+;); Calypogeia muelleriana (120: +); Bryum cuspidatum (121: +); Calliergonella cuspidata (121: +); Cephalozia lacinulata (121: +); Drepanocladus pseudostramineus (121: +); Meesia triquetra (121: +); Oncophorus wahlenbergii (121: +); Plagiochila asplenoides (121: +); Sphagnum fimbriatum (121: +); Drepanocladus lapponicus (123: +); Polytrichum juniperinum (123:+); Sphagnum majus (123:+; 125:+); Dicranum ontanense (191: +); Cladopodiella fluitans (125: +).

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The relative effects of various environmental gradients on the vascular plants and bryophytes was investigated in detail in the Lost River peatland of northern Minnesota. Three separate DCA ordinations were run to compare the response of the more deeply rooted vascular plants to that of the more shallow absorbing organs of the bryophytes: 1) the vascular plant scores (Fig. 21a), 2) the bryophyte scores (Fig. 21b), and the combined data set (Fig. 21c).

These three ordinations produce very similar results, indicating a similar response of the major plant types to water level and water chemistry. Most of the variation in the data sets is expressed along axis 1, which corresponds to a moisture gradient. The spring-fen relevés, which have the wettest surface, are grouped on the right side of this axis, whereas the drier forested stands are positioned to the left. The chemical gradient does not directly correspond to any of the DCA axes, but each of the vegetation types delineated by the ordination represents a distinct range in pH and calcium concentration. Thus the ordinations strongly support the vegetation types identified in the vegetation tables.

Canonical correspondence analysis (ter Braak 1986, 1987; Jongman *et al.* 1987) was used to approximate the quantitative relationship of the species and relevés to the environmental variables at Lost River. The species and relevés are indicated by points on the jointplot, whereas the environmental variables are plotted as arrows, which determine the axes of the diagram (Fig. 22). The weighted averages of the species with respect to the environmental variables are approximated by projecting a perpendicular line from each species point onto the axis of each environmental variable. The endpoints of these perpendiculars indicate the center of that species distribution (weighted average) along that particular environmental axis. Environmental variables with long arrows are more strongly related to the pattern of variation in the species composition than those with short arrows.

The CCA diagram for the relevés (Fig. 22) indicates that axis 1 most closely corresponds to the area of standing water (STAGW), which has the highest canonical coefficient (113) and inter set correlation (961) for axis 1 (Table 4). Tree cover has the

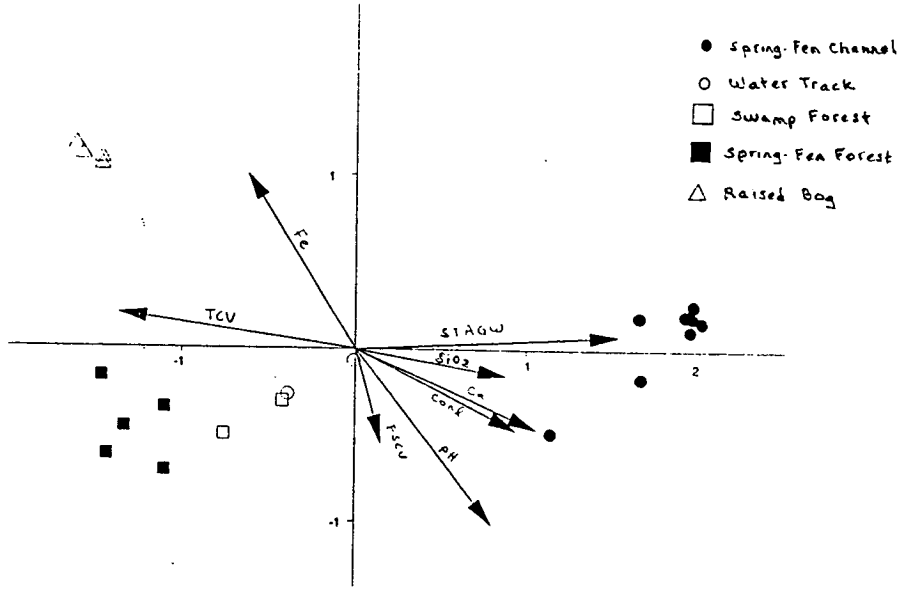
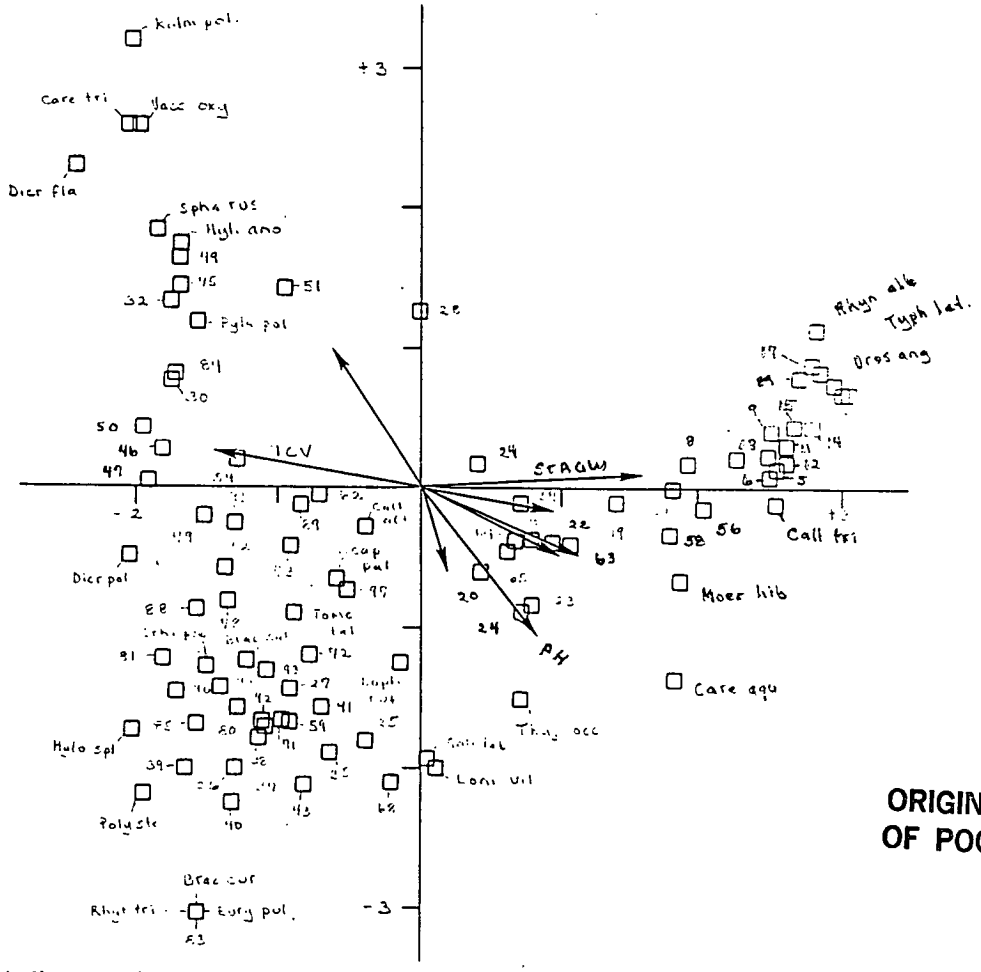


Figure 22. CCA ordination diagram of the Lost River vegetation relevés with the environmental variables represented by arrows. The environmental variables are: standing water (STAGW), conductivity (cond.), pH, Ca concentration (Ca), Fe concentration (Fe), SiO_2 concentration (SiO_2), tree cover (TCV), and forb/shrub cover (FSCV). The relevés are: spring-fen channel (SFC), spring-fen forest (SFF), swamp forest (SF), water track (WT), and raised bog (RB). The eigenvalues are 0.67291 for axis 1 and 0.22853 for axis 2. The diagram accounts for 65% of the variation of the weighted averages.



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Figure 23. CCA diagram of the species from the Lost River peatland with respect to the environmental variables. The numbers for the species points correspond to those in Tables 5 and 6. The symbols for the environmental variables and the eigenvalues are the same as those in Figure 22 (Glaser *et al.* in press).

strongest negative correlation to axis 1, and the direction of its arrow is nearly the opposite of that for standing water. Chemical variables, such as Ca concentration, conductivity, SiO_2 concentration, and pH, have progressively lower inter set correlations for axis 1. Ca concentration, however, has a very high variance inflation factor (VIF >21) indicating it is almost perfectly correlated with another factor, such as conductivity (VIF >9.5) and therefore has no unique contribution to the regression coefficient. These chemical variables are also related to pH (VIF >14).

Axis 2 most closely corresponds to Fe concentration, which has an inter set correlation of 692 (Table 4). The pH of the surface waters has the strongest negative correlation for axis 2 and the direction of its arrow on the ordination diagram is nearly the opposite of that for Fe.

The CCA ordination diagram for the relevés indicates that the spring-fen relevés have the highest weighted averages for standing water, whereas the spring-fen forest and raised bog relevés have the lowest (Figure 22). The swamp forest and water track relevés are centered at an intermediate position along this gradient but are located closer to the drier end. With respect to pH, the spring-fen relevés have the highest inferred weighted averages and the raised bog relevés the lowest, whereas the relevés from the spring-fen forest, swamp forest, and water tracks have intermediate averages.

The CCA ordination for the species (Fig. 23) shows the approximate center for the distribution (inferred weighted averages) of each species along the various environmental gradients at Lost River. *Muhlenbergia glomerata, Carex exilis, Drosera anglica, Typha latifolia,* and *Rhynchospora alba*, for example have the center of their distributions at the wettest end of the gradient for standing water (STAGW), whereas *Dicranum flagellare, Carex trisperma, Dicranum polysetum, Hylocomnium splendens,* and *Kalmia polifolia* are located at the driest end. For pH, *Kalmia polifolia, Carex trisperma, Vaccinium oxycoccos, Dicranum flagellare, Sphagnum russowii,* and *Mylia anomala* are respectively centered near the lowest values, whereas *Carex aquatilis, Moerckia hibernica, Calliergon*

trifarium, Thuja occidentalis, Lonicera villosa, and *Galium labradoricum* respectively are centered at the highest values. The labels for the species points in the ordination diagram correspond to the species in the vegetation tables (Table 5-6).

4.3. Hydrogeology and Peat Stratigraphy

An intensive hydrogeochemical investigation was conducted in the Lost River peatland, which contains the complete range in water chemistry and major landform-vegetation types within a very limited area. The study area of 780 hectares includes 3 different landforms 1) a spring-fen mound, 2) a raised bog, and 3) a narrow water track that separates these two peat mounds (Fig. 5). The crest of the spring-fen mound and raised bog are nearly at the same elevation although the spring-fen mound is located over a rise in the mineral substratum, and the bog occupies a depression (Almendinger *et al.* 1986; Fig. 5). The slopes are relatively gentle except for the slightly steeper drop on the eastern end of the spring fen. Peat depths range from about 2 m under the spring-fen mound to 3.3 m under the bog.

Both the spring fen mound and the raised bog are located in discharge areas for ground water despite their raised topography and significant accumulation of peat (Siegel & Glaser 1987). The hydraulic-head gradients at the crest and margin of the raised bog reversed seasonally in 1983, when the vertical direction of water movement changed from a downward to an upward direction in the peat column. When upward gradients prevailed, the entire peat mass swelled, raising the elevation of the benchmarks apparently as a response to a rise in pore pressure (Almendinger *et al.* 1986). The discharge of ground water within an apparently ombrotrophic bog is quite unexpected. This finding was nevertheless supported by the chemistry of the pore water under the bog, in which the pH and calcium concentration at 1 m depth were similar to the values found in the underlying calcareous till.

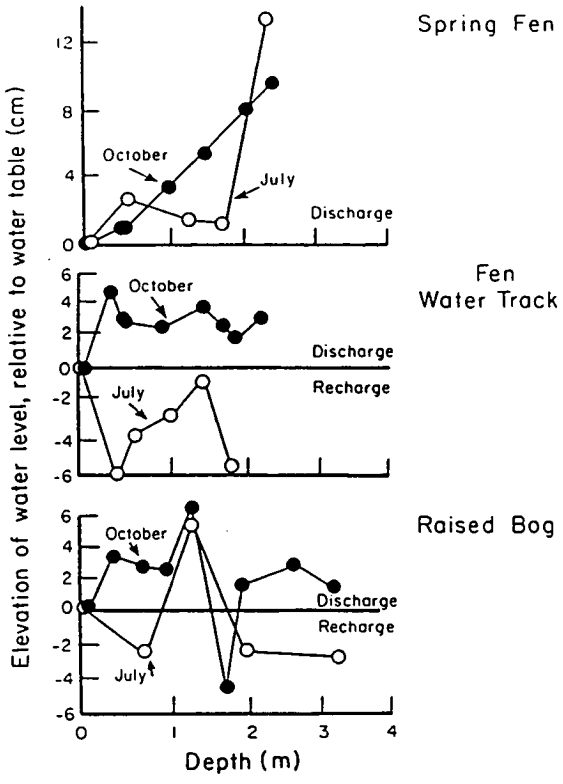


Figure 24. Water-level measurements in the Lost River peatland in mid-summer (0) and autumn (0) (Siegel and Glaser 1987).

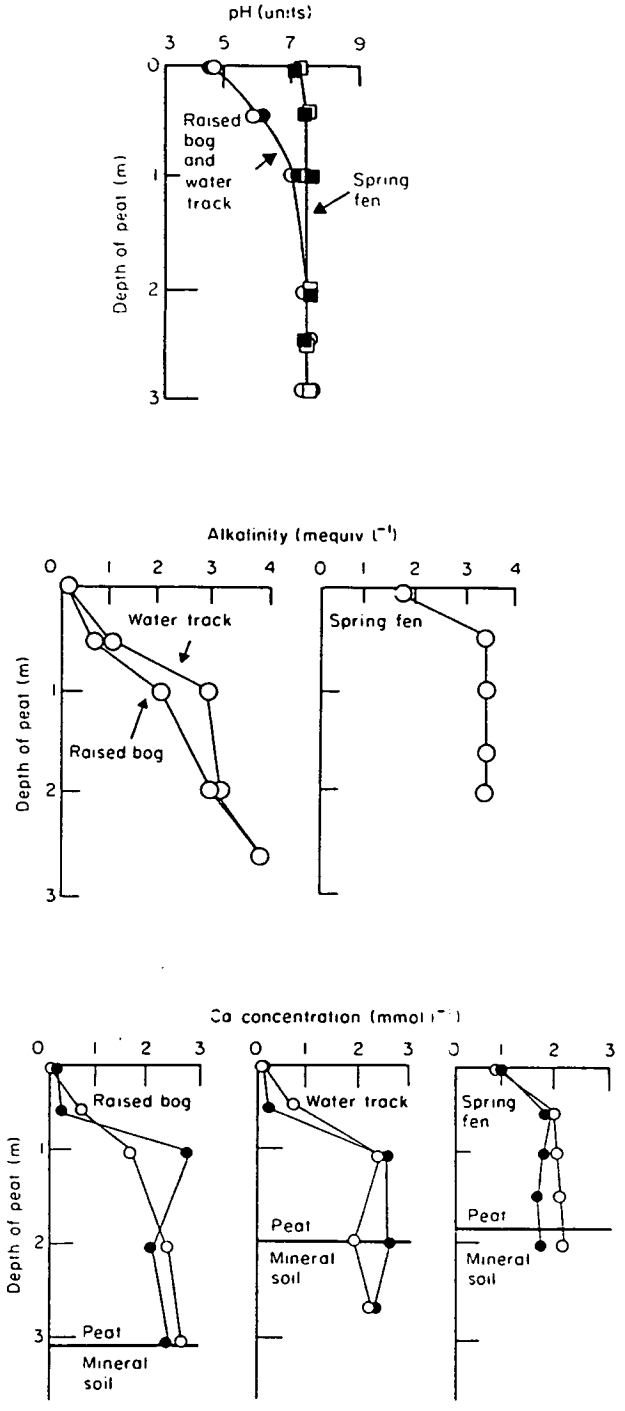


Figure 25. Depth profiles of the interstitial pore water at Lost River. The changes in pH (25a), alkalinity (25b), and calcium concentration (25c) are shown (Siegel and Glaser 1987).

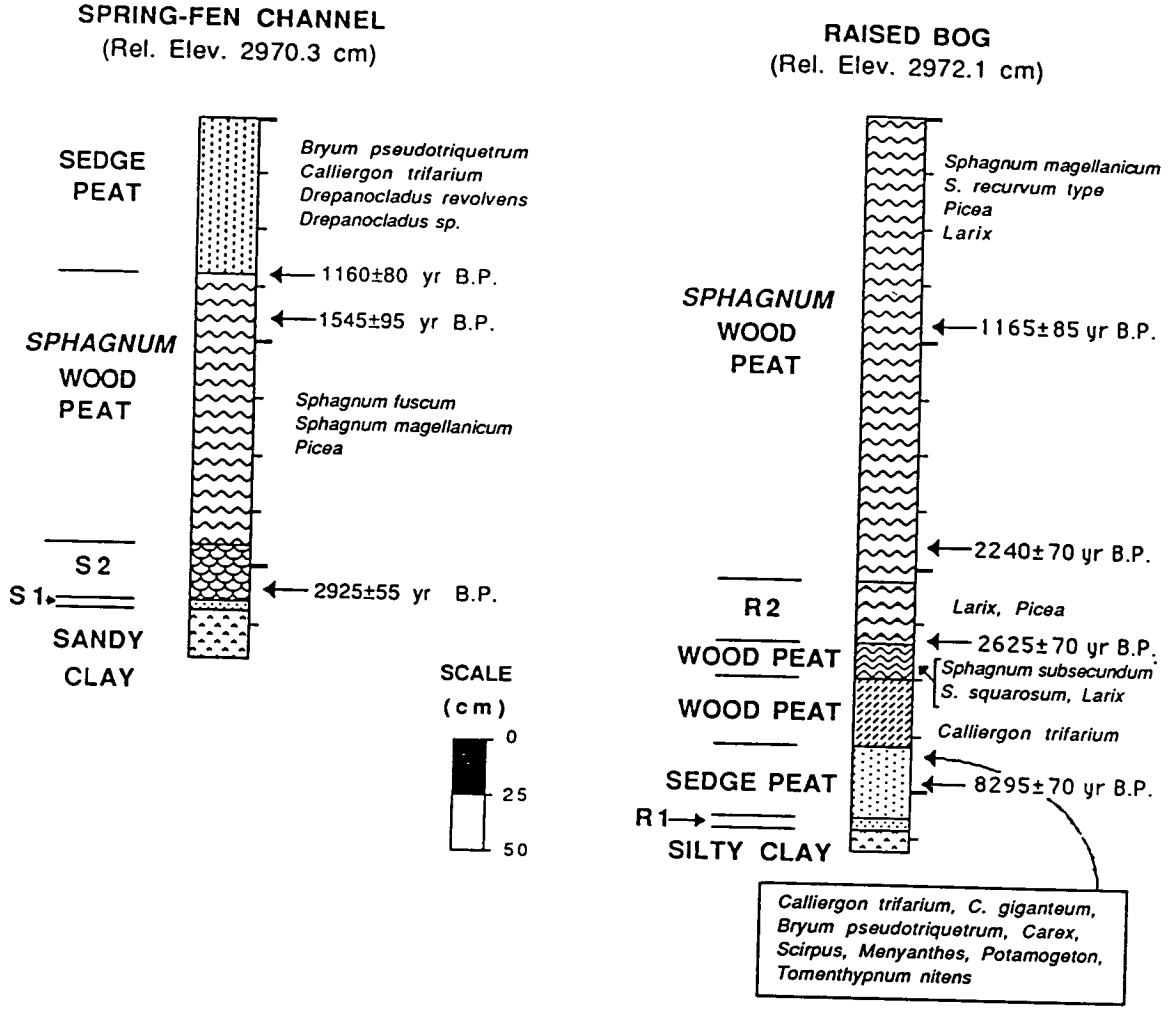


Figure 26. Peat stratigraphy from the spring-fen mound and raised bog in the Lost River peatland. The major peat types are labeled to the left of each core, and the most important macrofossils in each peat type are listed to the right. The hash marks on the right side of the cores indicate 25 cm increments. S1 represents a basal layer of highly decomposed peat in the spring-fen core and S2 represents a potentially detrital layer of woody *Sphagnum* peat. R1 represents a highly-decomposed layer of organic sediment in the bog core and R2 represents a woody *Sphagnum* peat with *Larix* needles (Siegel and Glaser 1987).

This study confirmed that the spring-fen channels were sites for groundwater discharge. The water levels in the piezometers were always above the elevation of the water table indicating upward head gradients (Fig. 24). The close similarity of these spring-fen channels with respect to vegetation, surface water chemistry, and landform to the other spring-fen channels across the 3 target areas indicates similar hydrogeologic conditions for all of these channels.

An unexpected finding was that the adjacent raised bog was also seasonally a discharge zone for groundwater (Fig. 24). Although the surface waters had virtually no alkalinity, a low pH (<4.2), and a low Ca concentration (<2 mg l^{-1}), the chemistry of pore water at 1 meter depth was identical to that in the underlying calcareous till (Fig. 25). Apparently the alkalinity carried by groundwater to the peat surface was consumed by organic acids or biotic processes within the top meter of peat.

The past response of the vegetation to hydrology at Lost River was reconstructed from the peat stratigraphy (Fig. 26). The two peat mounds in this peatland began to form about 2000 yr B.P. and rose in elevation at about the same rate. At this time both peat mounds were raised bogs but at 1200 yr B.P. one of these mounds was converted into a spring-fen channel. Apparently groundwater began to discharge at this site at that time. The deeper peat under the raised bog, however, swelled and the discharge rate was insufficient to alter the water chemistry and vegetation at the surface. Thus the 2 peat mounds at Lost River is delicately adjusted to the present hydrologic flow field and a slight change in the head gradient could produce significant changes in the vegetation.

4.4. Analysis with Landsat TM imagery

4.4.1. Vegetation Patterns

A greater range of vegetation types can be detected with false-color composites of Landsat TM imagery than from conventional aerial photographs. Bogs can clearly be distinguished from fens on the basis of their spectral characteristics, and the different types



Plate XXXI. Landsat image (2,3,4 = BGR) of peatland types in the Glacial Lake Agassiz region. The peatlands are dissected by mineral exposures (bright red) and by tributary streams (1) that direct the path of drainage. The large bog complex has a forested crest (2; dark purple) with lines of spruce radiating downslope. Fen water tracks (3; green) arise near the bog crest and divide the lower bog flanks into streamlined lobes. A much larger water track (4; green) arises from a sandy beach ridge (red) that is partially surrounded by a tamarack swamp. Flow lines in these water tracks are laminar and exhibit no evidence for turbulent mixing where the two tracks merge. These patterns indicate that the discharge of the main track is much greater than that of the smaller track. The image covers an area 12 km across. The arrows indicate the direction of flow.

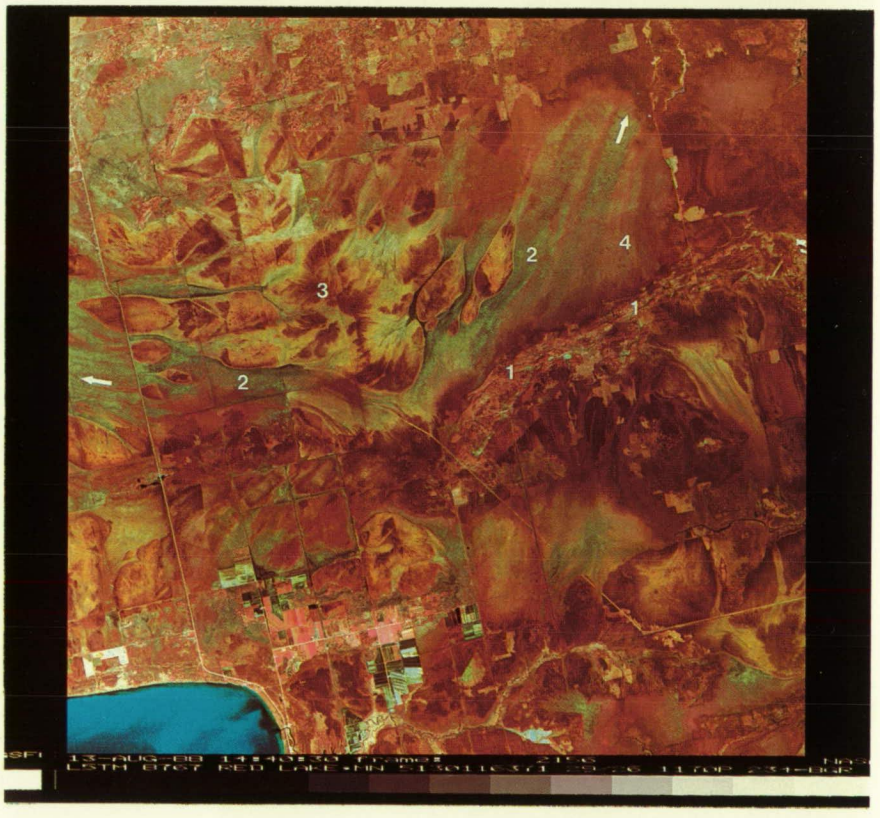


Plate XXXII. Landsat image (2,3,4 = BGR) of the Glacial Lake Agassiz peatlands in early fall (Sep. 1987). The peatlands are dissected by a sandy beach ridge (red; 1) from which large water tracks (green; 2) originate. Flow in these water tracks diverges around a large bog complex (brown-yellow; 3) that is situated over a drainage divide. Vegetation bands (4) in the water tracks indicate laminar lines of flow. The peatlands are locally cut by a grid of drainage ditches and by a powerline and roadways. The image covers an area approximately 20 km across. The arrows indicate the direction of flow.

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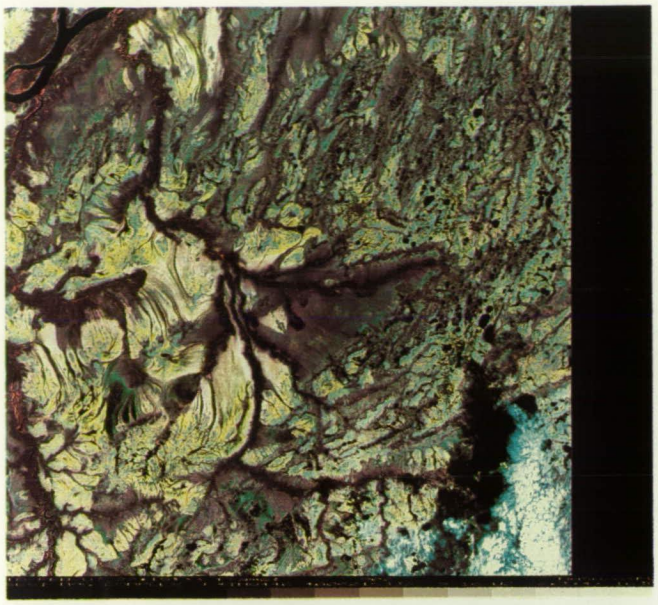


Plate XXXIII. Bogs and fens in the Albany River region. The Landsat TM image (2,3,4 = B,G,R) distinguishes large raised bogs that have lichen-covered crests (blue) and *Sphagnum* lawns (yellow) on their lower flanks. Poor-fen water tracks (green) can also be distinguished from the rich-fen swamp forests (purple); and the extremely-rich fen channels (turquoise). Nearly the entire image is covered by peat except for small mineral exposures (bright red), rivers (black), and small lakes (black) on the moraine complex to the right. The image covers an area approximately 50 km across.

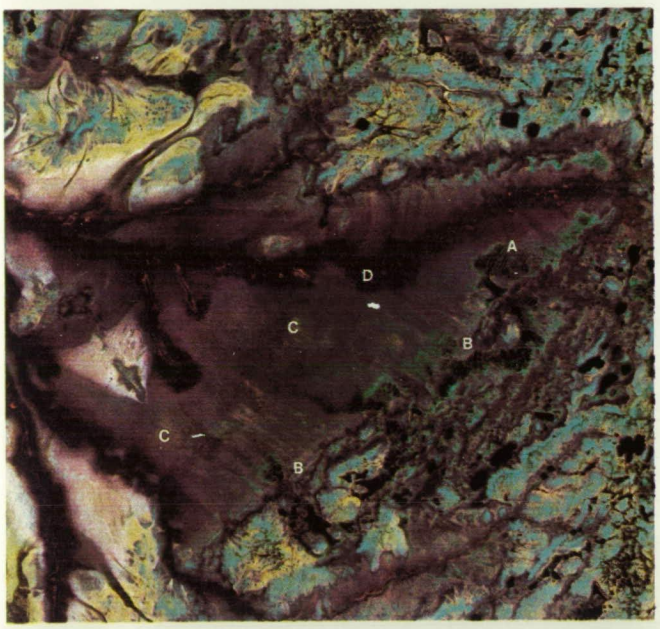


Plate XXXIV. Peatland patterns along the edge of a paludified moraine in the Albany River region. The colors on this subscene from Plate XXXIII indicate lichen-covered bogs (blue), *Sphag - num* bogs (yellow), poor-fen *Sphagnum* lawns (pink), poor-fen water tracks (green), rich-fen swamp forests (purple), and extremely-rich fen channels (turquoise). Numerous water tracks (A) arise from the edge of the moraine system (B) and discharge into the swamp forest (C). Laminar and "plumelike" flow lines are visible in the swamp forest leading toward a stream (D) at the edge of the watershed. The image covers an area 12 km across.

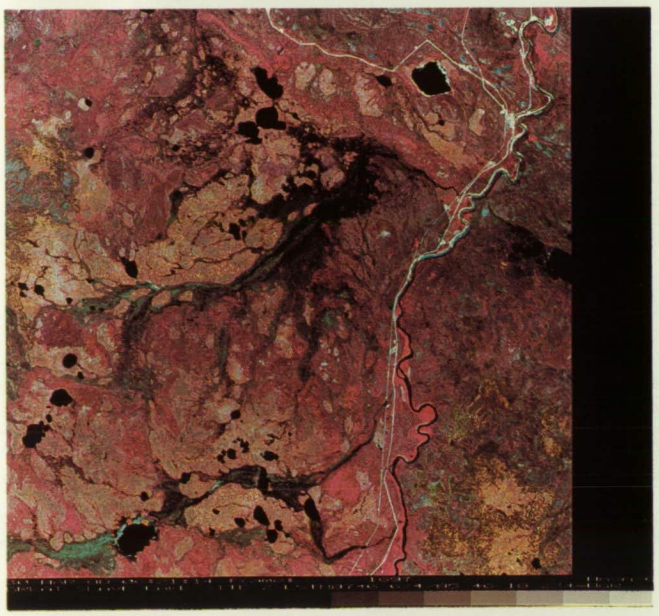


Plate XXXV. Peat plateaus in the Hay River region, N.W.T. The colors on this Landsat TM image (2,3,4 = B,G,R) indicate peat plateaus (orange), mineral exposures (red), and small lakes (black). Flow lines (blue-green; arrow) visible in the water tracks arise from the edge of the mineral uplands and diverge around the streamlined peat islands. This image covers an area approximately 37 km across.

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of bog and fen can be detected with TM bands 2, 3, and 4 (Plates 2,3,4,5, and 6). Although the spectral properties of these vegetation types change according to season and region, this variability is limited.

The dominant type of cryptogam on raised bogs can also be determined with Landsat TM imagery despite the presence or absence of trees (Plate 4 and 5). Bogs dominated by *Sphagnum* are clearly distinguished from those with high lichen cover in the 3 target areas. This distinction is significant, because the *Sphagnum*-covered bogs appear to be accumulating carbon much more rapidly than bogs dominated by lichens (Glaser and Janssens 1986). The Landsat imagery also provides a sensitive indicator for the transition from bog to poor fen on the *Sphagnum* lawns that form an apron around the lower bog flanks and bog margins.

The major types of fen vegetation may also be distinguished on Landsat images composed of TM bands 2, 3, and 4. In the Albany River region, the spectral properties of extremely rich fens (pH> 6.8; Ca concentration> 20 mg l^{-1}) are different from those of poor fens (pH 4.2-5.5; Ca concentration 2-10 mg l^{-1}), although both of these vegetation types are dominated by sedges (Plate 4 and 5). In the Hay River region, extremely rich fens, may also be distinguished on false-color composites with TM bands 3, 4, and 5 (Plate 6). In the Glacial Lake Agassiz region, extremely rich fens are too small to be detected on satellite imagery. However, the spruce (*Picea mariana*) swamps that surround them have a different spectral signature than the rich fen swamps dominated by tamarack (*Larix laricina*).

Landsat imagery provides an important means to distinguish bog from fen vegetation in areas where the peatlands contain large pools. In the Albany River area, for example the bog landforms commonly have large networks of deep pools, which appear uniformly black on conventional aerial photographs. Without a detailed ground survey it is impossible to determine whether the pool networks are part of the bog matrix or represent

fen water tracks. On the color-composite Landsat images, however, the fen pools are distinguished by their green tones.

4.4.2. Distribution of the Major Vegetation Types

The Landsat scenes provide a synoptic view of the vegetation patterns with respect to the important physiographic features in the three target areas. In the Glacial Lake Agassiz region, mineral exposures are common throughout the peatlands and play an important role in determining the peatland vegetation patterns (Fig. 3, Plate 2). Fen vegetation predominates in areas where sandy beach ridges dissect the peatlands, whereas bog vegetation forms the most important cover type in areas where the exposures are largely composed of silty-loamy or clayey ground moraine (Figs. 2 and 15).

The close relationship between soils and the spatial spread of bogs is demonstrated by an analysis of the mire complex types. Mire complexes that are primarily composed of bog (types 1,2,5) are surrounded by clayey or loamy soils that have a relatively low hydraulic conductivity (Fig. 15). Mire complexes that have large areas of fen (types 3, 4, 6, 7,10,), however, are consistently surrounded by sandy outwash or beach ridges. The largest water tracks in Minnesota, such as those at Red Lake and Myrtle Lake all arise downslope from these sandy beach deposits.

Regional changes in soil types have a dramatic effect on the size and abundance of water tracks. In the northeastern portion of the Glacial Lake Agassiz region raised bogs nearly cover the peatlands, which generally can be identified as type 1 or 2 mire complexes (Fig. 3). This region is largely covered by relatively impermeable clayey lake sediments. An outlier of sandy outwash, however, is associated with the head of the large water track at North Black River. In the southeastern portion of the Lake Agassiz region the bog complexes (type 3, 5, and 8) are almost completely surrounded by larger water tracks and featureless swamp forests. The peatlands in this zone are only locally interrupted by narrow sandy beach ridges.

To the east the beach ridges almost disappear underneath the Red Lake peatland, where large bog complexes have developed over drainage divides in the eastern and central watersheds. Here most of the landscape is covered by bog, but the bogs are finely divided by water tracks that arise from the lower bog flanks. The extremely large western watershed at Red Lake, however, is almost completely composed of fen vegetation, including the huge western water track. The edges of this watershed are marked by exposures of sandy outwash and beach ridges. This relationship is continued in the northwestern part of the Lake Agassiz peatlands. This area contains the largest patterned fens in Minnesota, which are surrounded by sandy outwash and beach deposits. Only a few bogs occur in this region despite the large expanse of peatlands.

The regional distribution of bog and fen is therefore closely related to the texture of the adjacent soils. Peatlands are dominated by bogs where the adjacent clayey or loamy soils are relatively impermeable. Mire complexes, however, are dominated by fens when the adjacent mineral exposures consist of porous sandy outwash or beach ridges. These deposits are always found near the source of the largest water tracks or spring fens. The most likely explanation for this relationship is that the sandy deposits are conduits for alkaline groundwater discharging from the calcareous soils that underlie the peatlands.

The tributary streams that dissect these peatlands also play an important role in determining the orientation, location, and stability of the peatland patterns. The large water tracks generally drain toward the heads of tributary streams that are slowly eroding headward into the peatlands. The orientation of the vegetation patterns, however, may change as new tributary streams cut into the margin of the peatland and alter the direction of drainage. This process is apparent in the North Black River peatland (Glaser 1983a) and the northern edge of the western water track in the Red Lake peatland, where trees and shrubs are growing over former drainage paths. The tributary streams also seem to control the position of several large bogs, which are located between two adjacent streams.

In the Albany River study area, the physiographic controls on peatland development are more subtle, because the landscape is nearly completely covered by peat. Nevertheless, the distribution of bog and fen vegetation in this area is not uniform and exhibits a strong relationship to physiography. A classification of the data from Landsat TM bands 2, 3, and 4 in the Albany River region indicates that the majority of these peatlands are fen (56%) with a smaller area of bog (34%) and a much smaller area of standing water (10%) (Fig. 3). The major blocks of fen vegetation are located downslope from the moraine complexes, which are almost entirely covered by lichen-covered bogs. Therefore fens may be supplied by alkaline ground water that discharges from the edge of the moraine complex, because a surface source for this alkalinity is lacking. This hypothesis is supported by finer-scale TM imagery described below. The large areas of bog, in contrast, are located on the dissected plain to the west, where the bogs occupy divides between the tributary streams.

In the Hay River region, the distribution of bogs and fens does not seem to be strongly related to physiographic features. The lowlands are dominated by large bog complexes (peat plateaus) that are underlain by permafrost (Fig. 9). These bogs are dissected by a fine dendritic network of fen water tracks that occasionally converge into a large single track. Some of these large water tracks arise near the margins of mineral exposures, but others originate from within the peat plateaus. Peat plateaus are also the most important peatland type on the flanks and summits of the Caribou Hills, where they are dominated by lichens.

4.4.3. Hydrogeochemical Processes

The hydrogeochemistry of these large peat basins may be inferred directly from the vegetation patterns, which are sensitively adjusted to both the hydrology and water chemistry. The Landsat TM imagery provides new data for predicting 1) the location of regional seepage faces for ground water, 2) relative volumes of groundwater discharge, 3) flow dynamics in watersheds with very low rates flow, and 4) tests for various models of

peatland hydrology. The intensive study of the hydrogeology and peat stratigraphy of 2 peat mounds in northern Minnesota documented the hydrologic flow fields associated with the vegetation patterns.

4.4.3.1. Discharge zones

Discharge zones for groundwater are generally characterized by 1) anamolies in the surface water chemistry and 2) characteristic peat landforms in these large peat basins (Glaser et al. 1986; Glaser 1987a, b). Alkaline surface waters (pH> 6.8; Ca concentrations > 20 mg l^{-1}) generally indicate zones where groundwater is discharging from the calcareous sediments that underlie these peat basins. Without the continual discharge of ground water these surface waters would soon equilibrate to a lower pH (about 5.6) as CO_2 from the atmosphere diffuses into the water. The most common landforms associated with these alkaline waters are spring-fen channels and water tracks with reticulate networks of pools and peat ridges (Fig. 12). The discharge of groundwater has been documented by hydrogeologic methods in a spring-fen channel from northern Minnesota (Siegel and Glaser 1987), and these results should apply to the other spring-fen channels in these peat basins, which have strikingly similar vegetation and landform patterns. The discharge of groundwater may also produce fen water tracks (pH> 5) or expanding lakes (pH 4.5-5) within the interior of acid bogs (pH< 4.2). However, the water chemistry from these sites is insufficient by itself to conclusively document discharge.

Discharge zones for groundwater (extremely rich fens) can be distinguished by their spectral properties with Landsat TM imagery, particularly in the Hay River and Albany River target areas. In the Albany River region, discharge zones seem to be concentrated along the edge of the moraine complexes, producing a regional seepage face for groundwater (Plate 5). Discharge zones also seem to be located along the downslope edge of large raised bogs in this area. In the Glacial Lake Agassiz region the largest water

tracks and blocks of fen vegetation are concentrated downslope from sandy beach ridges (Fig. 2; Plate 3). The high porosity of these sand deposits also make them a likely source for upwelling groundwater.

Strong support for this hypothesis is provided by Landsat TM imagery taken during the spring break-up (Fig. 27). At this time the water tracks are open and flowing, while the surrounding raised bogs and mineral soil are still frozen and snow-covered. The most likely source for the heat necessary to melt the ice in these water tracks is ground water upwelling from the underlying mineral soil. This imagery also indicates that the water tracks are fed by systems of narrow channels that originate near the margins of the beach ridges (Fig. 10). These channels dissect tamarack swamps that have a distinctive spectral signature on the Landsat imagery (bands 2, 3, and 4) taken during late September (Fig. 3).

4.4.3.2. Flow lines

The direction of surface drainage in these peat basins may be detected by the orientation of the vegetation patterns in plan view, despite the nearly level slope and imperceptible rates of flow. Streamlined peat landforms are always oriented parallel to the prevailing slope, with their rounded heads facing upstream and tapering tails trailing downslope. The networks of pools and peat ridges in the water tracks, in contrast, are consistently oriented perpendicular to the slope. The Landsat TM imagery also detects linear patterns in the water tracks that seem to represent flow lines for runoff (Plates 2,3,5, and 6). These patterns are most conspicuous in water tracks of the Hay River region, with false-color composites composed of TM bands 3, 5, and 4. These "flow lines" are generally laminar, particularly where they diverge around streamlined bog islands. However, they tend to dissipate in areas where the water track contains conspicuous networks of pools and peat ridges (Plate 6).

In the Albany River region both laminar and tortuous flow patterns are detectable in swamp forests with false color composites utilizing TM bands 2, 3, and 4 (Plate 5). They

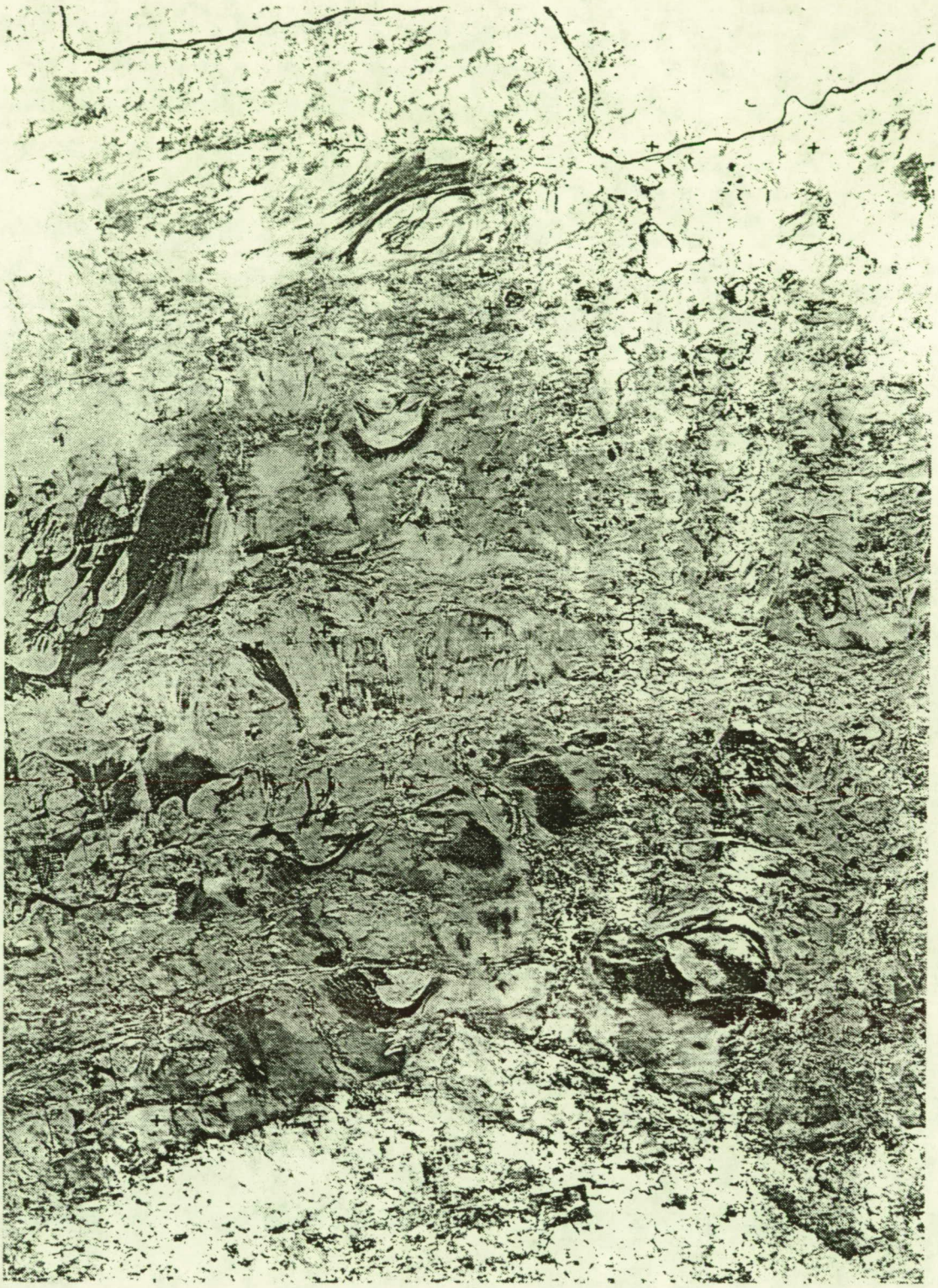


Figure 27. Landsat MSS image of the Glacial Lake Agassiz peatlands during spring break-up of 1978. The white tones on this image are snow-covered bogs, swamp forests, and exposures of mineral soil. The darker tones are water tracks with flowing water. These water tracks flow around the streamlined margins of large bogs. Smaller "internal" water tracks are also located within the interior of the larger bogs. The image covers an area approximately 70 km across and is just east of the area shown in Fig.10.

seem to represent subtle vegetation patterns that respond to local changes in the water chemistry and flow dynamics. They can be traced from their source at the edge of moraine complexes toward tributary streams at the margin of these watersheds. These flow patterns cannot be detected with conventional aerial photographs that depict a relatively featureless stand of vegetation. Similar types of flow lines are also present on Landsat imagery of the Glacial Lake Agassiz peatlands.

4.4.3.3. Discharge volume

Although Landsat TM data cannot be used to directly measure rates of flow or volumes of groundwater discharge, they nevertheless provide 1) estimates for relative volumes of flow and discharge and 2) precise locations for hydrological field sampling. In the Albany River region the TM imagery discerns flow patterns imperceptible on conventional aerial photographs. Along the edge of moraine complexes, spring fens and water tracks discharge into broad swamp forests and drain toward tributary streams at the edge of the watershed (Plate 5). The size of these channels should be proportional to their volume of flow, which controls their flux of cations and prevents them from being invaded and overrun by *Sphagnum*. Most of the small narrow channels can only be traced a short distance downslope where they fade into the surrounding swamp forest. The larger channels, however, have much longer trajectories and continue to the edge of the watershed. In contrast, the largest water track produces a large plume-like pattern that tapers into a single flow path downslope.

Landsat TM imagery also provides an indication of relative flow rates where 2 water tracks converge. In the Glacial Lake Agassiz region, for example there is no indication for turbulent mixing where two water tracks merge at right angles (Plate 2). This pattern suggests that the main track has a much larger volume of flow than its smaller tributary.

5. Discussion

Most concepts of peatland hydrogeochemistry and ecology have been developed by mire ecologists working in relatively small peatlands. These concepts have been applied by default to the large peat basins of North America, which probably represent one of the most pristine and least studied ecosystems of North America. These peat basins, however, are ideally suited for a regional analysis with Landsat TM imagery because of their great expanse and their unique vegetation patterns. These vegetation patterns have been termed peat landforms because of their remarkable regional uniformity and consistent shapes (Glaser *et al.* 1981; Glaser 1987 a,b).

5.1. Peat landforms

The peat landforms provide important indicators for the processes that control the development of these large peat basins. First, the shape and spectral properties of these landforms are closely correlated with particular vegetation assemblages, narrow ranges in water chemistry, and different types of peat stratigraphy (Glaser *et al.* 1981, Glaser and Janssens 1986; Glaser 1983a, 1987a, b). Second, the landforms are closely adjusted to hydrology. Certain types of landforms indicate discharge zones for groundwater and the orientation of the patterns sensitively indicate lines of flow (Glaser *et al.* 1986; Glaser 1987a, b). Third, spatial transitions from one type of landform to another indicate potential developmental trends that may be tested by the stratigraphic analysis of peat cores (Glaser *et al.* 1981; Glaser 1987b). Fourth, the quantitative analysis of the landform shapes may be used to infer the processes that formed them (Glaser 1987a). Fifth, the spatial scale of these landforms (10^2 to 10^4 m^2) is suitable for the regional analysis of biotic and hydrogeochemical processes using Landsat TM imagery.

Although the peat landforms are detectable with conventional aerial photographs, the Landsat TM imagery provides essential new data for their interpretation. The analysis of Landsat data products indicates that the major physical and biotic processes that control the

development of these peat basins may be quite contrary to concepts developed in smaller peatlands.

5.2. Hydrogeochemical controls

5.2.1. Regional seepage faces

A central concept of peatland hydrology states that water flow is restricted to the uppermost portion of a peat profile where the peat is relatively porous and undecomposed (Ingram 1983). At greater depths the peat is believed to be impermeable to flow because of its high degree of decomposition and correspondingly low porosity. According to this concept the input of water and salts into a peatland should be restricted to 1) precipitation and 2) runoff from mineral exposures.

In the large peat basins of North America the regional spread of peatlands greatly restricts the area of mineral exposures. As this source of alkalinity decreases, raised bogs should spread over the landscape, because there is insufficient alkalinity in precipitation to stop the spread of *Sphagnum*. *Sphagnum* will then acidify the peatland as a result of its cation exchange system or release of organic acids.

Information derived from Landsat TM imagery, however, disproves this hypothesis. In the Glacial Lake Agassiz region the peatlands are predominantly covered by fens except where the exposures of mineral soil changes from sandy beach deposits to loamy or clayey ground moraine. In the Albany River region the landscape is almost entirely covered by peat but the peatlands consist mostly of fen vegetation. The source of the alkalinity in these fens seems to be supplied by the discharge of groundwater upwelling from regional seepage faces at the edge of the moraine complexes or beach ridges. Thus, the accepted concepts of peatland hydrology do not seem to be applicable to the large peat basins of North America where permafrost is absent.

This hypothesis is supported by the hydrogeologic data from the Lost River peatland. The nonforested channels on the spring-fen mound at Lost River are very similar to the

spring-fen channels elsewhere. The great similarity among these features in terms of their peat landforms, water chemistry, and vegetation indicates that they are all located in discharge zones for groundwater.

In the Hay River region, the predominance of bog complexes (peat plateaus) is probably controlled by the distribution of discontinuous permafrost. Permafrost will block the flow of subsurface water and locally raise the elevation of the peat surface. Nevertheless, the Landsat imagery indicates that water tracks in this area may be fed by the discharge of groundwater. Conspicuous flow lines are visible in these water tracks that arise near mineral exposures, lakes, or within the interior of bog complexes (Plate 6). The spectral signature of these flow lines on the Landsat imagery and their very high alkalinity (pH> 7-8) in places indicates that they may also be supplied by groundwater upwelling from the calcareous mineral soil that underlies these peatlands.

5.2.2. Local seepage faces

The conventional concept of peatland hydrology states that raised bogs are completely isolated from groundwater because 1) their surface is elevated above the flood level of water in the adjacent fens, and 2) their dense accumulation of humified peat is impermeable to groundwater flow. The interpretation of Landsat TM imagery, however, indicates that all the larger bogs (>20 km^2) within these boreal peat basins are dissected by fen water tracks that arise near the bog crest (Glaser 1987a). The alkalinity in these water tracks rises downslope but never reaches the level (pH> 7) where it is diagnostic of calcareous groundwater. Apparently the volume of groundwater discharge is insufficient to raise the pH to the extremely-rich fen range (Siegel and Glaser 1987).

The Landsat TM and MSS imagery, however, provides strong evidence that these fen water tracks are supplied by alkaline groundwater. During the time of spring break-up these water tracks generally thaw first, while the surrounding area of bog is still frozen (Fig. 10, 27; Glaser 1987b). This effect is apparent in both the Hudson Bay lowlands and

the Glacial Lake Agassiz region. The most likely heat source to melt these water tracks preferentially is groundwater upwelling from the mineral substrate underneath these peatlands.

5.3. Feedbacks between hydrology and vegetation succession

5.3.1. Groundwater effects

The seepage faces for ground water have two principal effects on vegetation succession in these large peat basins. Along regional seepage faces the upwelling of groundwater prevents the spread of acidifying *Sphagnum* and maintains large stands of fen vegetation (Fig. 2-3, 28). This result is unexpected, because conventional concepts of peatland succession predict that these areas should be converted into a continuous expanse of bog. In local areas, however, upwelling groundwater may supply the alkalinity necessary to convert strips of bog into fen vegetation. This phenomenon has been documented from the peat stratigraphy in northern Minnesota (Glaser 1987b; Glaser *et al.* in press), and may be a common feature for bog development within large boreal peat basins. The conversion of a bog into a fen runs counter to conventional principles of peatland succession (Glaser 1987a).

Siegel (1981, 1983) has suggested that the growth of raised bogs on these flat plains may produce sufficient differences in hydraulic head to drive local flow cells. The development of water table mounds under the raised bogs may drive local flow cells in which the water flows downward from the bog crest into the underlying calcareous till and then rises to discharge in the adjacent water tracks. Landsat TM imagery from the Albany River region supports this hypothesis by indicating that large water tracks arise around the downslope margins of large bogs.

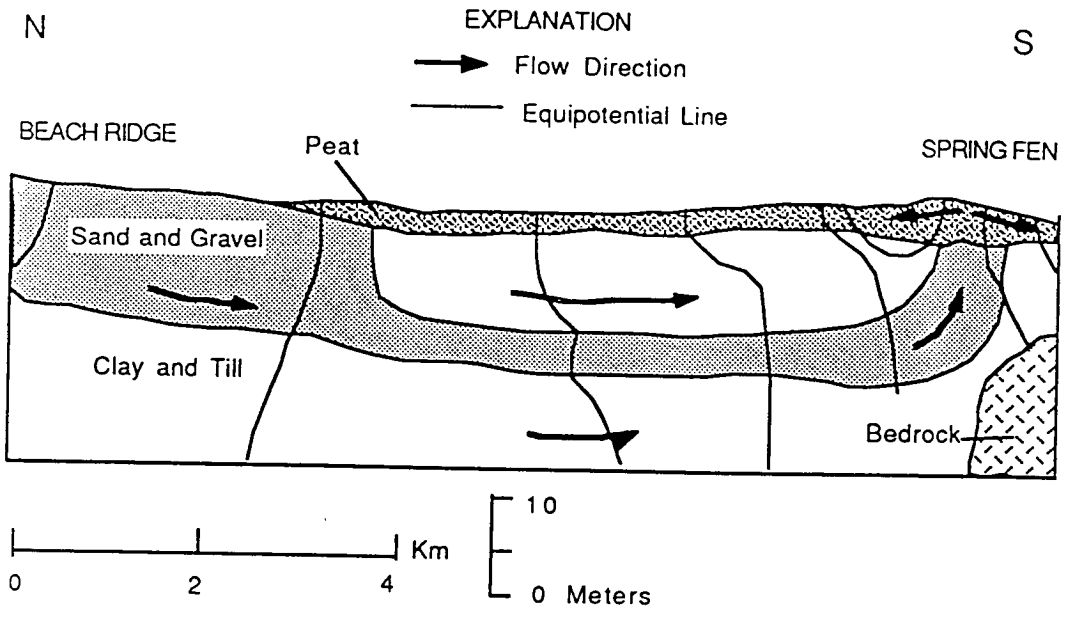


Figure 28. Model for groundwater flow in the Glacial Lake Agassiz region. The discharge zones for groundwater may be controlled by 1) permeable lenses of sand in the glacial till that underlies the peatlands and 2) topographic high points in the bedrock.

5.3.2. Vegetation patterning

The streamlined bog and fen patterns in these peat basins appear to represent a stable adjustment of the vegetation to the hydrology and water chemistry. The physical dimensions (length, width, and area) of the streamlined bog islands, for example, are strongly correlated and appear to represent equilibrium features (Glaser 1987a) (Fig. 29). The length-to-width ratio of these vegetation patterns (1:3) also corresponds to the ratio that would produce the minimum drag or resistance to flow in a wind tunnel or flume (Komar 1983, 1984). Glaser (1987a) suggests that the most stable configuration of these peat islands is one that minimizes turbulent mixing in the adjacent water tracks and permits a boundary layer with low alkalinity to form around the island margin.

This hypothesis is difficult to test by standard hydrologic methods because of the nearly imperceptible flow in the water tracks. The Landsat TM imagery, however, provides new data to evaluate the dynamics of flow in the larger water tracks. The vegetation patterns detectable on color composites of TM bands 2, 3, and 4 or 3, 4, and 5 are generally laminar and show no signs of turbulent mixing. In the Albany River region, however, two types of flow patterns appear where water tracks and spring-fen channels discharge into a swamp forest (Fig. 5). Most of the flow lines are laminar, but the largest water track has a pattern similar to a turbulent wake. In this area a large volume of groundwater may have recently discharged onto the peatland and disrupted the existing vegetation pattern. The vegetation in this area may eventually adjust to these new flow conditions by establishing a water track with laminar flow patterns.

The development of laminar drainage patterns in these peatlands seems to be the product of a sensitive feedback system involving the response of the major peat-formers to the hydrology and water chemistry (Glaser 1987a,b) (Fig. 30-31). Water tracks develop where surface drainage contains sufficient alkalinity to promote the growth of sedges, such as *Carex lasiocarpa.* These peat formers produce very porous peat, which further channels drainage into these zones. Runoff, however, is diverted around the margins of the

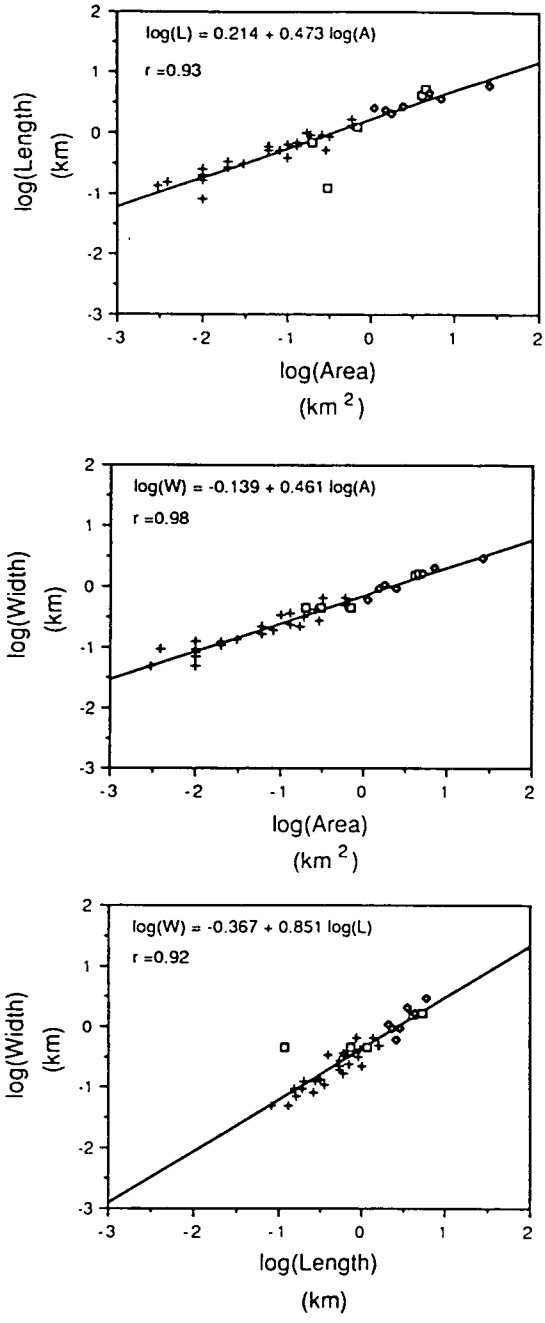


Figure 29. Morphometric analysis of streamlined bog islands. Islands from the Pigeon River in Manitoba are shown by crosses, islands from watershed IV (*sensu* Glaser *et al.* 1981) at the Red Lake peatland in northern Minnesota by boxes, and islands from watershed II (*sensu* Glaser *et al.* 1981) at Red Lake by diamonds.

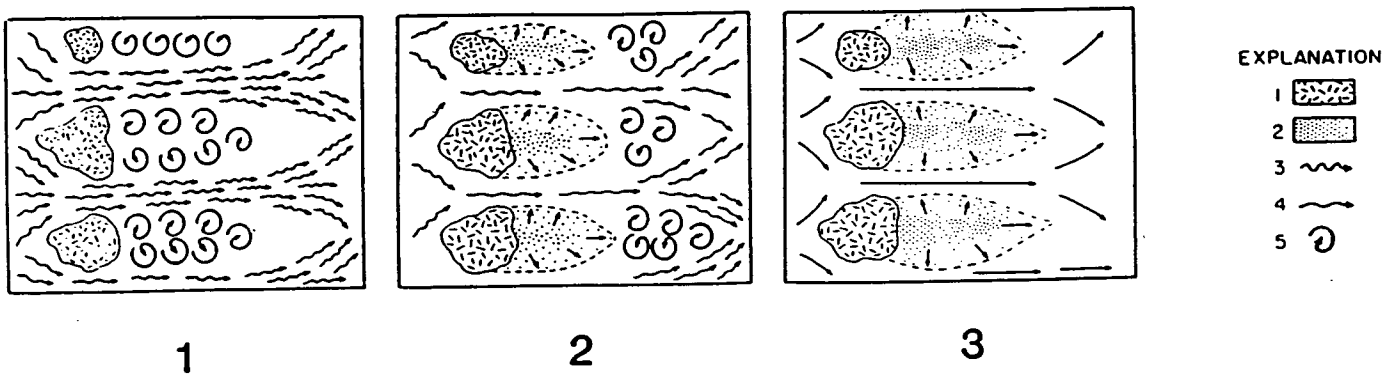


Figure 30. Developmental model for bog islands and water tracks (Glaser 1987a).

1) As peat spreads over a landscape the path of runoff is diverted around obstructions (crystalline rock outcrops) creating zones of sluggish flow downslope (circular arrows, step 1).

2) As peat continues to accumulate Sphagnum mats form in these zones of sluggish flow where the alkalinity and flux of cations is low (step 2).

3) The Sphagnum mat will spread outward until its continued growth is checked by the higher alkalinity transported by the main path of flow (step 3).

4) Runoff continues to be channeled into the water tracks because of the great difference in hydraulic conductivity between the Sphagnum peat under the bogs and more porous sedge peat under the water tracks (step 4). The symbols indicate 1) mineral outcrops, 2) Sphagnum mats, 3) tortuous flow, 4) streamlined flow, 5) zones of sluggish flow.

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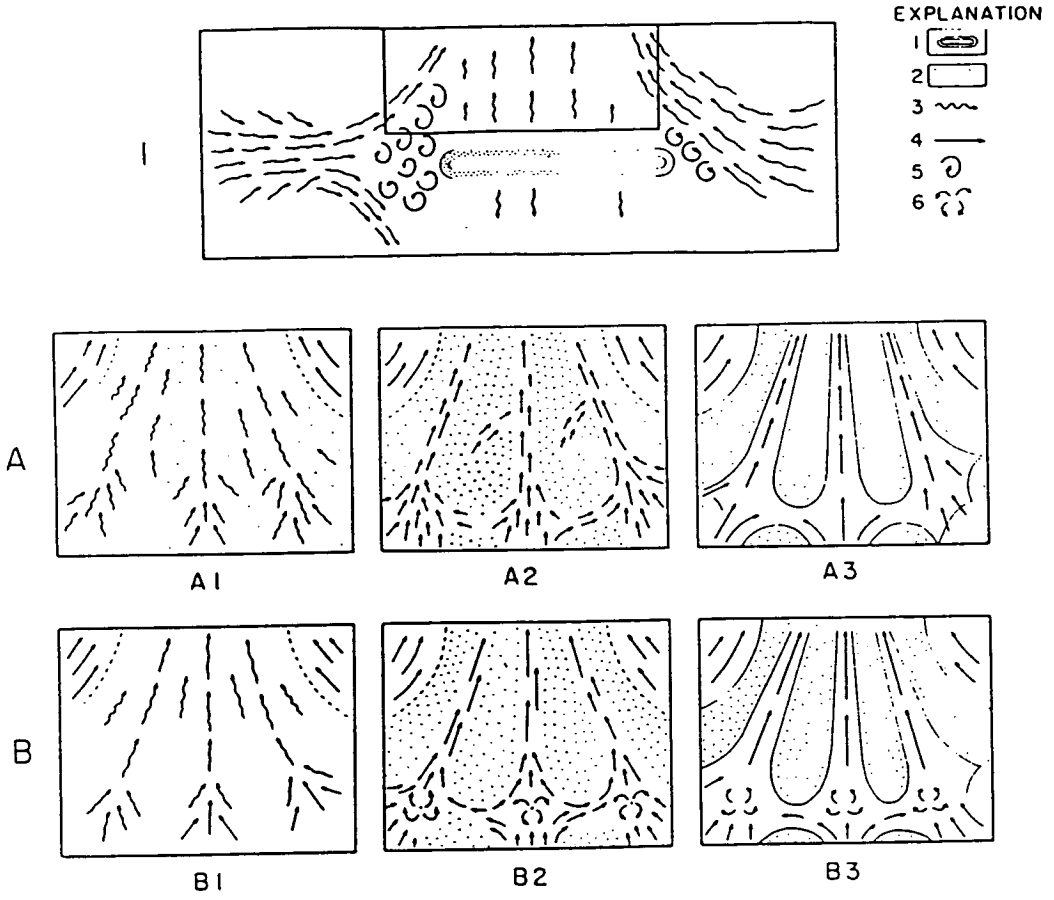


Figure 31. Developmental model for a raised bog complex (Glaser 1987a).

A large (>20 km^2) bog complex forms as runoff is diverted around a large obstruction creating a large zone with sluggish flow (step 1). Sphagnum will colonize these zones and spread out to form a continuous mat. The mat will then be fragmented by water tracks (A and B). According to the corrosive oxidation hypothesis a base is released by enhanced decomposition along lines of flow (A_1 - A_3). A base can also be transported from the underlying mineral soil by the discharge of ground water (B_1 - B_3). Once at the surface the higher alkalinity in these waters promotes the localized growth of sedges and the channeling of runoff into water tracks that are dominated by sedges. The symbols are described above with the exception of 1) mineral beach ridge and 6) discharge zone for ground water.

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Sphagnum bogs, because the *Sphagnum* peat is relatively impermeable. The boundary between a bog and water track is determined by the intolerance of the bog *Sphagnum* for the alkalinity in the water track and the corresponding intolerance of the major fen peat-formers for the low alkalinity in the *Sphagnum* bog. The bog/fen boundary will then shift as the alkalinity and volume of flow changes in the water tracks.

6. Conclusions

Landsat TM imagery indicates that the discharge of alkaline ground water is largely responsible for the development of vegetation patterns in the large peat basins of North America. Regional seepage faces for ground water are located along the margins of sandy beach deposits or paludified moraine systems and produce large areas of minerotrophic fen. The more localized discharge of ground water may also produce the fen water tracks that dissect all the larger (>20 km^2) raised bogs of these peat basins. Contrary to conventional concepts of peatland ecology and hydrology, these large peat basins seem to be sensitively adjusted to the dynamics of groundwater hydrology, which may radically alter the expected path of peatland succession.

Although the vegetation landforms within these major peat basins are visible on aerial photographs, Landsat TM imagery provides essential new evidence for their analysis. Spectral data from the Landsat TM system provides (1) synoptic views of the patterns across large portions of these peat basins, indicating important physiographic controls on peatland development, (2) more sensitive detection of the major vegetation types, allowing rapid quantitative estimates to be made of their distribution and aerial extent, (3) discrimination of bog areas with potentially rapid or slow rates of peat accumulation, (4) identification of discharge zones for groundwater, which apparently represents the most important source of alkalinity in these peat basins, and (5) detection of flow patterns in water tracks that appear nearly uniform on standard aerial photographs.

These large peat basins seem to be ideally suited for study by Landsat TM imagery, because of 1) the large relatively uniform stands of vegetation and 2) the intimate feedback systems that have developed between the vegetation and hydrogeochemical processes.

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8. List of Publications

Journal Articles

Glaser, P.H., J.A. Janssens, and D.I. Siegel. (In Press). The response of vegetation to hydrological and chemical gradients in the Lost River Peatland, northern Minnesota Journal of Ecology.

Glaser, P.H. 1989 Detecting ecologic and hydrogeochemical processes in large peat basins with Landsat TM imagery. Remote Sensing of Environment 28: 109-119.

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Book Chapters

Glaser, P.H. (in press). Peat landforms. *In* H.E. Wright, Jr. and B.A. Coffin (eds.), Patterned Peatlands of Northern Minnesota, University of Minnesota Press, Minneapolis.

Glaser, P.H. (in press). Vegetation and water chemistry. *In* H.E. Wright, Jr. and B.A. Coffin (eds.), Patterned Peatlands of Northern Minnesota, University of Minnesota Press, Minneapolis.

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Janssens, J.A., B.C.S. Hansen, P.H. Glaser, and C.W. Barnosky. (in press). Development of a raised-bog complex in northern Minnesota. *In* H.E. Wright, Jr. and B.A. Coffin (eds.), Patterned Peatlands of Northern Minnesota, University of Minnesota Press, Minneapolis.

Papers Submitted

Glaser, P.H. Patterns of species richness and floristic composition on raised bogs in eastern North America. (submitted to the Journal of Ecology).